

Ecology and Ethno-ornithology of Black Kites *Milvus migrans* in Delhi, India

Thesis submitted for the degree of Doctor of Philosophy

Michaelmas Term 2018 -19



Nishant Kumar
Somerville College and the Department of Zoology
(Edward Grey Institute of Field Ornithology)
University of Oxford
&
Wildlife Institute of India
(Department of Animal Ecology & Conservation Biology)

This thesis is dedicated to the numerous citizens of the societies in the developing countries, where religiously ascribed empathy and cultural expressions to the animal species in a shared ecosystem need equal (if not more) conservation attention.

(Below, I mention a quintessential verbatim)

मेरे पास गिद्धों, एवं बाकी पक्षियों के विलुप्त हो जाने के दुःख को बयां करने के लिए शब्द नहीं हैं मैं बस इतना कह सकता हूँ कि आस-पास के जीवों के लुप्तप्राय होने पर ठीक वैसा ही महसूस होता है, मानो कोई अपना गुज़र गया हो।

आप उस दर्द का इज़हार शब्दों में नहीं कर सकते!

I have no words to describe the feeling, having witnessed the local extinction of vultures and many other species of birds. If I try, I can only equate this loss with the death of someone close.

You can't describe (model) the grief in words!

DECLARATION

I, hereby, declare that this dissertation, titled, "**Ecology and Ethno-ornithology of Black Kites *Milvus migrans* in Delhi, India**", constitutes original research conducted by me under the supervision of Prof. Andrew G. Gosler, faculty member at the University of Oxford, and Dr. Fabrizio Sergio, faculty member at the Doñana Biological Station, CSIC; Spain. The thesis has been submitted to the University of Oxford for the award of the degree of Doctor of Philosophy in Zoology, and has not formed the basis for the award of any other degree. It embodies my own work and observations; and in that respect, the investigation advances knowledge on the subject.



Place: Oxfordshire
Date: 11.01.2019

Nishant Kumar
(D. Phil. Candidate)

Countersigned:



Andrew G. Gosler, D. Phil.
(Supervisor)



Fabrizio Sergio, D. Phil.
(Co-Supervisor)

ACKNOWLEDGEMENTS

I would like to thank my supervisors, Dr. Andrew Gosler and Dr Fabrizio Sergio for their guidance and support. This study began in a very nurturing mentorship of Dr. Fabrizio Sergio, Prof(s). Y V Jhala and Q Qureshi, effectively leading to a M.Sc. dissertation in 2012-13. The preliminary inferences paved way for a long-term inquiry (Black Kite Project is running through its fifth phase: 2018 to 2020), beginning with a doctoral dissertation in 2014. My D. Phil. advisory committee members Prof(s) Y. V. Jhala, Qamar Qureshi, Tom Pizzari and Chris Perrins are acknowledged for their valuable inputs. Faculty members, friends and colleagues at the Edward Grey Institute, Somerville College, and the Wildlife Institute of India are acknowledged for crucial and thoughtful discussions. Dr. Alessandro Tanferna, Prof. Ben Sheldon and Prof. B Harriss-White helped, and provided guidance on research aspects. I would like to thank the trustees, members and advisors of the Felix Scholarship Trust, Somerville College, Raptor Research and Conservation Foundation, Mumbai, Microwave Telemetry USA, Edward Grey Institute and WII for funding and supporting the project. Special thanks to R. Naoroji, K. Srivastava, Kim Ooi, Dr. Franz Kuemmeth and Marc Buentjen for constant support. Dr. Fabrizio also aided the project with biologgers and other equipment, afforded from the multiple grants: Project RNM-7307 of the Junta de Andalucía and CGL2015- 69445-P of the Spanish Ministry of Economy and Competitiveness. My project supervisors from WII aided the fieldwork with trail cameras, binoculars, handheld GPS units, etc.

I would also thank Ujjwal Kumar, and the Director, Dean and research coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. Delhi Police, and the Forest Departments of Delhi and Uttar Pradesh, Delhi Transport Corporation, Civic bodies of the Government of NCT of Delhi helped with legal permits, and the Director of the National Zoological Park of New Delhi gave access to study kites in the Park. Miranda House College and University of Delhi allowed access to their campus for nest monitoring. We express our most heartfelt gratitude to more than 100 researcher, interns and volunteers of the “Black Kite Project Group” from WII, University of Delhi (Sri Venkateswara and Deshbandhu Colleges), especially U Gupta, H. Malhotra, A. Singh, P. Kumar, Y. Taneja, M. Kalita, A. Mehta, M. Singh, Rubina, Urjaswi and N Kumar, who provided essential field help,

enthusiasm and cooperation in the environmental education of locally assembling crowds of curious people. Special thanks to our field assistants Laxmi Narayan, Prince Kumar and Poonam, who were the backbone of the field team. Finally, thanks to all the landowners, managers and government officials who patiently cooperated with our constant requests of access.

My heartfelt gratitude shall go all the well-wishers: support staff at OxZoo (Heather, Lynne, Sharon, Caitlin, Reception Staff, IT Zoology, Alexander Library, Darwin's), Somerville (Potter's lodge, Academic Office, Senior Tutor, College Tutors), WII (Tiger Cell, academic and administrative staff, library staff, dining hall, other support staff), families of my supervisors, and at various institutions in Delhi for taking keen interest in my study, and offering all the possible help. No words can ever express my gratitude to my own family members (especially my siblings) who are pillars of my strength. Lastly, thanks to the birds and citizens of Delhi. Researching this system has been so enjoyable!

Abstract

Rapid worldwide urbanization is generating a steep growth in studies on urban ecology, but tropical cities have had extremely scarce attention. To fill this gap of knowledge, in this thesis, I studied a dense population of an avian predator and facultative scavenger, the Black Kite *Milvus migrans*, breeding within Delhi, a 16-million-inhabitants megacity. I studied the ways in which this species managed to adapt, respond and exploit such an extreme urban environment by running analyses at individual as well as population-level, through sampling at 28 independent plots, stratified and (randomly) scattered, to cover all the urban configurations present in Delhi. In particular, I focused on the dependence of this population on anthropogenic subsidies, afforded as human waste (in the streets or at refuse tips) and as intentional “ritual offerings” of meat scraps for religious purposes, especially by people of Islamic faith that are concentrated in “Muslim settlements”. I found that the kite breeding population was stable over the past five decades, with a diet strongly dominated by human subsidies, especially ritual offerings, and with an extremely high density that makes it the largest raptor concentration of the world. Kites were not randomly distributed in the city but over-selected areas with high human density, poor waste management and a road configuration that facilitated ready access to resources provided by humans, in particular to Muslim colonies that provided ritual subsidies. Rather than a nuisance to avoid, as previously portrayed, humans were thus a keenly-targeted foraging resource. These individual-level preferences translated into population-level effects, with kite density tightly tied to Muslim subsidies. This relationship was further modulated by nest-site availability, mainly in the form of tree availability, which paved the way to potential population-manipulation through tree management. Ecological responses were accompanied and mediated by behavioural adjustments to the urban gradient, which not only provided adaptive benefits but also generated potential conflicts with humans. In particular, offspring defence was finely-tuned on human subsidies, probably as a result of the associated parental investments and familiarity with humans. In its most extreme form, nest defence led to attacks on humans, sometimes with serious physical harm. I show that such aggression was tied to frequent exposure to humans by kites while accessing their ritual subsidies and by constant close proximity to them while breeding, as caused by local architecture (balconies in the immediate proximity of nests). Despite the conflict, I also report the extremely benevolent attitudes of local people to the attacking kites, typical of southern-Asian cultural beliefs, but extremely unusual for western urban standards. Finally, I show how the stunning predator densities observed in Delhi are generated by the local breeding subspecies, but also by thousands of Black-eared Kites of the migratory *M. m. lineatus* subspecies that settle in Delhi during their wintering, non-breeding period. Through GPS-tagging, I found that they migrate to Delhi from their breeding quarters of Russia, Kazakhstan, China and Mongolia through a 3300-4700 km migration in which they regularly cross the Himalaya range at elevations of up to 5000-6000 m a.s.l., an aspect hitherto unknown. I discuss all my findings in terms of their contribution to broadening our views of urban ecology so that it is more inclusive of patterns and processes that better characterize the tropical cities of non-western nations. In particular, all my results stress the overriding importance of incorporating human socio-cultural factors in urban ecological studies.

INDEX

Sl.	Section and Chapters	Page #
1	General Introduction	1 - 13
	References & Supplementary material	
i.	Density, laying date, breeding success and diet of Black Kites <i>Milvus migrans govinda</i> in the city of Delhi (India)	14 - 58
	Abstract	
	Introduction	
	Materials and Methods	
	Results	
	Discussion	
	References & Supplementary material	
ii.	Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools	59 - 85
	Abstract	
	Introduction	
	Materials and Methods	
	Results	
	Discussion	
	Conservation Implications	
	References & Supplementary material	

iii. Offspring defense by an urban raptor responds to human subsidies and ritual animal-feeding practices 86 - 101

Abstract

Introduction

Materials and Methods

Results

Discussion

References & Supplementary material

iv. Human-attacks by an urban raptor are tied to human subsidies and religious practices 102 - 115

Abstract

Introduction

Materials and Methods

Results

Discussion

References & Supplementary material

v. The population density of an urban predator is inextricably tied to human cultural practices 116 - 127

Abstract

Introduction

Materials and Methods

Results

Discussion

References & Supplementary material

vi GPS-telemetry unveils the regular high-elevation crossing of the Himalayas by a soaring raptor: implications for definition of a “Central Asian Flyway” 128 - 140

Abstract

Introduction

Materials and Methods

Results

Discussion

References & Supplementary material

2 Synthesis 141 - 162

References & Supplementary material

3 Appendix [Typescript Journal Articles (2) and two Comic Booklets in *English* and *Hindi*]

1.

General Introduction

Urbanization has achieved a major landmark in its history with the majority of people now living in cities (United Nations, 2014). Despite well recognised threats of rapid urbanisation to biodiversity, there remains a paucity of ecological studies from tropical megacities. These cities are supposed to face the burden of persistent and steeply growing urbanization over the coming decades. This problem takes on yet further dimensions in the context of ever increasing technological changes (e.g. over ground power transmission line networks, mobile towers, wind turbines, high rise buildings with intense lights, etc.). Rapid urban sprawl has consequent impacts on the energy flow and nutrient cycles of urban ecosystems, which further get accentuated by a rise in the built up area and habitat degradation (e.g. McKinney, 2010; Pickett et al., 2001).

A wide variety of organisms, and many birds, have co-existed with humans for centuries as urban exploiters or *anthropo-dependent* commensals (Hulme-Beaman et al., 2016). However, a subtle oversight regarding effect of increased urbanization is reflected in the changing direct and indirect contact these ‘citizens’ have with nature, as cities becomes sinks to the immigrating humans from the rural areas (Crane & Kinzig, 2005). As a long-term effect, it is likely that socio-cultural shifts will increase urban-versus-rural disagreement on priorities for backyard biodiversity. This disagreement is even further reflected in urban political ecology which factors decisions constituting ‘appropriate’ wildlife or habitat management. While urban ecological research has already investigated various selection pressures offered by urban-rural gradients within human dominated systems, research on tropical urban ecosystems and their constituent components has been scanty (Crane & Kinzig, 2005). In such a context, studies on

the organisms which form the apex trophic level in urban ecosystems become extremely important.

Birds exhibit some of the most spectacular spatial displacements to accomplish their daily and periodic activities (e.g. Newton, 2008). Owing to the stringent and acute requirements through these journeys, they have recently become a good model system to study anthropogenic impacts due to shifts in their phenologies and life history parameters (Tryjanowski et al., 2013). Rapid restructuring of urban biological communities (e.g. sympatric competitors, facultative migrant scavengers), and stochastic shifts in the role of *anthropodependent* species (see Hulme-Beaman et al., 2016) are a major concern for rapidly populating cities in the global South (United Nations, 2014). Compared to their rural counterparts, these long and short-term changes modify the behavioural profiles of the individuals interacting with urban ecosystems (Isaksson et al., 2018). Therefore, studies involving commensal birds as model species offer opportunities to investigate the proximate drivers of evolutionarily crafted daily and periodic life history strategies. While research on urban ecology grows exponentially (e.g. Mayer, 2010), most studies have focused on cities of the developed world, which may function in profoundly different ways compared to those of developing countries. In particular, there is a paucity of intensive studies conducted in tropical regions (a severe deficiency highlighted by many reviews, (e.g. Chace & Walsh, 2006; Magle et al., 2012; Marzluff, 2017), despite the fact that rapid urbanization is heavily concentrated in such areas (Grimm et al., 2008; Malakoff et al., 2016).

In the Indian megacity of Delhi, tens of thousands of Black Kites (*Milvus migrans*, hereafter “kite”), live on the food and other waste made available to kites in intentional and unintentional manners by more than 16 million people. This is probably the largest raptor concentration in the world (Galushin, 1971; Kumar et al., 2014; Naoroji, 2011). By scavenging, and therefore removing waste, kites provide services essential to the health of urban people, both locally and in much of the developing world. Thus, birds such as vultures and kites acquire special significance for people (Ninan, 2009). However, the cultural value of birds in general, and of these commensal birds of prey in particular, extends far beyond the utilitarian. Because south Asian socio-religious diversity, complex interplays of colonization, modernization, urbanization, and technification, have, over four centuries, caused biological extinctions and severed many connections people enjoyed with nature, the disconnection occurring today is unprecedented (Louv, 2006). To address these dynamics, I proposed this interdisciplinary study to document key aspects of cultural knowledge and response to a prominent raptor species in Delhi. Focusing on the experience and traditions of residents of historical Muslim neighbourhoods, I investigated the ecological consequences of these important bird-human relationships. By bringing local perspectives into the available research on urban ecology, I aimed to seed important, two-way relationship of perception: from the side of a facultative scavenger as it adapts to a typical urban life, and the citizens responding to their presence. The quintessential rationale of this research programme was adding quantitative estimates to aid our understanding of the role of human socio-cultural behaviour in shaping urban ecology, by documenting folk-culture and history of valuing diverse ecological knowledges.

The significance of Delhi

Delhi is a megacity of more than 16 million inhabitants, currently covering an area of 1500 km² and in constant, rapid expansion (Census organization of India, 2011). Predicted to be the largest global megacity by 2050 with more than 50 million inhabitants, it is polycentric and heterogeneous, with a multitude of juxtaposed biocultural contexts. One such juxtaposition is the close association of abattoirs and Muslim communities (Sharan, 2014). Urban scavengers such as kites and vultures have historically functioned as vital commensals as they quickly remove meat offal from meat-processing areas. Two aspects of Delhi are important for human-bird interactions (Kumar et al., 2018). First, large areas, usually overlapping with dense human settlements, have poor solid waste management, which affords abundant food such as carrion and organic refuse to animals (e.g., rodents, crows, sparrows, pigeons etc.). Secondly, people (primarily in Muslim communities) engage in a centuries-old practice of feeding meat scraps to kites (so called “ritualized feeding”). These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries (Pinault, 2008). Thus, waste management issues common to all communities, and cultural rituals which are more specific to some, generate spatial heterogeneity in the potential food availability for birds, and constitute a positive feedback loop between ecosystem services and cultural perceptions inducing reverence for these birds. Most importantly, prior quantitative data for this biogeographic region are extremely scarce and previous studies on kites in particular, all of them conducted in the 1970s, have focused on: (1) a coarse estimation of the size of the overall Delhi population (Galushin, 1971), and (2) data on the breeding ecology of a single high-density colony located in the Delhi Zoo (Desai & Malhotra, 1979).

The significance of Black Kites (in context of the recent local collapse of White-backed Vultures)

The Black Kite is a medium-sized opportunistic scavenger, widely distributed throughout Eurasia, Africa and Australia, and considered to be the most successful raptor in the world. Its relationship with humans ranges from active avoidance in Europe to close coexistence with them in Afro-Asia, and the species is synanthropic in India as a city scavenger (Ferguson-Lees & Christie, 2001), occurring in close association with people in towns and cities. Kite distribution and abundance have likely responded to changed spatial distributions of habitat and food sources within Delhi, and may have acquired a portion of the niche previously occupied by vultures prior to their population collapse (see below) in the Indian Subcontinent (Prakash et al., 2003). Kites also contribute by predating rodent pests with consequent benefits for human health (Kumar et al., 2014). In Delhi, kites sometimes form loose colonies, locally reaching extremely high densities thanks to their use of human food ‘subsidies’ facilitated by inefficient refuse disposal and by religious kite-feeding practices. These large-scale subsidies may explain Delhi’s capacity to host what is probably the largest raptor concentration in the world (Kumar et al., 2014, 2018).

As this thesis deals with a facultative scavenger species, spending a few words on the recent Indian vulture crisis seems necessary. The Indian sub-continent has been home to nine species of vultures. However, by the year 2000 the region virtually lost its principle avian scavenger, the White-backed Vulture *Gyps bengalensis* (Prakash et al., 2003). The densest livestock population in the world, maintained under poor sanitation around human habitation (Ministry of Agriculture, 2012), allowed vulture populations to thrive in Delhi. Estimated at over 40 million individuals in the country, they primarily occupied all the landfills and carcass

dumping locations of the Delhi capital. Since about 1990, however, vulture numbers have declined by 97% because of carcasses that often contained the veterinary drug Diclofenac, which is fatal for vultures (Prakash et al., 2003). The collapse raised serious issues for waste management and human health, but has also affected the people dependent on its eco-cultural services, e.g. the Parsi community who practiced *dokhmenishini* (“sky burials”: see van Dooren, 2010). In urban areas, while the vulture niche has been partially filled by kites and dogs (Markandya et al., 2008), citizens still actively associate the act of scavenging with vultures. Although a ban on Diclofenac and emergency conservation-programmes have been enacted in breeding areas, recovery of the vulture population is still far off. Through this thesis, and under the vision of a long term project in general, I aimed to investigate the ecology of the new main scavenger species of the Delhi urban ecosystem after the vulture collapse. This project also aimed to identify people's perceptions and knowledge of vultures' loss, their response to this population collapse, and acknowledgement of any associative changes in kite numbers at the landfill and in the city in general.

Aims and structure of this thesis

This thesis aimed to investigate the adaptations of a medium-sized raptor to a highly urbanized landscape and the variation of its outcome in terms of breeding success. I dedicated a special focus to the impact of urban structures and waste disposal systems to investigate the relationship between Black Kite density, breeding success and urban planning. The dissertation was planned as a comprehensive assessment of the response of Black Kites to an urban gradient within the megacity of Delhi. The study, currently monitoring the seventh breeding season of resident breeding kite populations in Delhi, is based on a framework of survey-plots that covers most of the observed urbanization gradients, ranging from fully rural to intensively urban settings. Field activities were structured to cover the whole gradient in a continuous manner, i.e. with points scattered all along the gradient rather than through a simplistic dual comparisons between urban vs rural sites. Supplementary material for each data chapter has been provided after the references. Credits for the images, data and figures used in the thesis have been mentioned, unless they are my own. Below, I briefly expose how the thesis has been structured.

1. Chapter 1 introduces and quantitatively describes the natural history and breeding ecology characteristics of the study population of the resident Black Kite subspecies *Milvus migrans govinda*. Here, I report comprehensive quantitative data on density, nest spacing, phenology, breeding success and diet. Subsequently, I compare the current estimates with historical records and with studies on other kite sub-species. This chapter, already published in the journal *Bird Study* (<https://doi.org/10.1080/00063657.2013.876972>), is presented in this thesis with an updated sample of 780 nests monitored through the breeding seasons of 2013 - 2018.

2. In **Chapter 2**, I examined the urban, ecological and human factor that affect nest-site selection along the urbanization gradient, as tested through the comparison of breeding habitat attributes between 154 kite territories and 154 random locations. In addition, I examined the effect of these variables on breeding success and on the rate of territory occupancy, used as an estimate of territory quality. This chapter has already been published in the journal *Urban Ecosystems* (<https://doi.org/10.1007/s11252-017-0716-8>)

3. In **Chapter 3**, I focused on a behavioural trait that may mediate kite responses to urbanization, namely the protection of the offspring by parents when “threatened” by humans approaching their nest. This chapter has already been published in the journal *PLoS ONE* (<https://doi.org/10.1371/journal.pone.0204549>).

4. In **Chapter 4**, I examined the consequences of human-kite interactions, focusing on the peculiar case of aggressive attacks towards humans by kites when defending their nestlings. Here, I modified the analysis of Chapter 3 to compare aggressive pairs that attacked humans with non-aggressive pairs while controlling for the confounding effects of territory quality, season, and previous research-visitation. This chapter is **in press** in the journal *Scientific Reports* (DOI:10.1038/s41598-019-38662-z).

5. In all previous chapters, the focus has been mainly on individual-level responses to urbanization. In **Chapter 5**, I tested how population-level density responds to urbanization. Here, the large number of plots sampled through the years along the whole urbanization gradient allowed me to apply multivariate models and examine which components of urbanization affect population-level properties. This chapter will build heavily on the analyses of Chapter 2 on individual-level nest-site selection, up-scaling them to the population-level. **This chapter is** now published in *Proceedings of the Royal Society: B* (DOI:10.1098/rspb.2018.2932).

6. **Chapter 6** is the last data chapter and is based on GPS-tagging of the migratory *lineatus* subspecies of the Black Kite. Thousands of individuals of this kite subspecies winter within Delhi, in sympatry with the *govinda* subspecies, which is the main subject of this dissertation. Chapter 6 will be soon submitted to a general ecological journal. Note that during the thesis development, I had occasion to participate to a paper that is directly related to Chapter 6 and which assessed the potential impact of GPS-tagging on Black kites, using data from an intensive tracking-study on a Spanish population. I participated to the statistical analyses of this assessment, as part of my training into radio-tagging, afforded by Dr. F. Sergio and his research group, and aimed at familiarizing myself with radio-tagging techniques and GPS-data processing in order to re-apply these techniques to my Delhi study population. The assessment led to a co-authored paper published in the *Journal of Applied Ecology* (reference: Sergio, F., Tavecchia, G., Tanferna, A., López Jiménez, L., Blas, J., De Stephanis, R., Marchant, T.A., **Kumar, N.** & Hiraldo, F. 2015. No effect of satellite tagging on a raptor survival, recruitment, longevity, productivity, social dominance, and its offspring provisioning and condition. *Journal of Applied Ecology* 52: 1665-1675; <https://doi.org/10.1111/1365-2664.12520>)

Chapter 6 is now published in *Scientific Reports* (DOI:10.1038/s41598-020-72970-z).

In the **Final Section (Synthesis)**, I recapitulate the findings of all the six data chapters, framing the thesis as the beginning of a long-term study on this species response to urbanization. In particular, I also outline some of the future research themes that I am already developing as part of the ongoing **Phase V (2018- 2020)** of the **Black Kite Project**, funded by the Raptor Research and Conservation Foundation of Mumbai (India) and by the Wildlife Institute of India.

Synthesis is now published in *Economic & Political Weekly*, 54 (47) 42 - 47.

References

- Census Organization of India. (2011). Census of India. Available from: <http://censusindia.gov.in/2011census>. [Accessed on 25.12.2018].
- Chace, J.F., & Walsh, J.J. (2006) Urban effects on native avifauna: a review. *Landscape and Urban Planning* 74: 46-49
- Crane, P., & Kinzig, A. (2005). Nature in the Metropolis. *Nature*, 5726(1225).
- Desai, J. H., & Malhotra, A. K. (1979). Breeding biology of the pariah kite *Milvus migrans* at Delhi zoological park. *Ibis*, 121(3), 320-325.
- Ferguson-Lees, J., & Christie, D. A. (2001). Monk vulture: *Aegypius monachus*. *Raptors of the World*, 437-438.
- Galushin, V. M. (1971). A huge urban population of birds of prey in Delhi India. *Ibis*, 113(4), 522-522.
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., & Briggs, J.M. (2008) Global change and ecology of cities. *Science* 319: 756-760
- Hulme-Beaman, A., Dobney, K., Cucchi, T., & Searle, J. B. (2016). An ecological and evolutionary framework for commensalism in anthropogenic environments. *Trends in ecology & evolution*, 31(8), 633-645.
- Isaksson, C., Rodewald, A. D., & Gil, D. (2018). Behavioural and Ecological Consequences of Urban Life in Birds. *Frontiers in Ecology and Evolution*, 6, 50.
- Kumar, N., Gupta, U., Jhala, Y. V., Qureshi, Q., Gosler, A. G., & 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 Ecosystems*, 21(2), 339-349.
- Kumar, N., Mohan, D., Jhala, Y. V., 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), 1-8.
- Louv, R. (2006) Last Child in the Woods. *Algonquin Books*, N. Carolina.

- Magle, S. B., Hunt, V. M., Vernon, M., & Crooks, K. R. (2012). Urban wildlife research: past, present, and future. *Biological conservation*, 155, 23-32.
- Malakoff, D., Wigginton, N. S., Fahrenkamp-Uppenbrink, J., & Wible, B. (2016). Rise of the urban planet. *Science*.
- Markandya, A., Taylor, T., Longo, A., Murty, M. N., Murty, S., & Dhavala, K. (2008). Counting the cost of vulture decline—an appraisal of the human health and other benefits of vultures in India. *Ecological economics*, 67(2), 194-204.
- Marzluff, J. M. (2017). A decadal review of urban ornithology and a prospectus for the future. *Ibis*, 159(1), 1-13.
- Mayer, P. (2010). Urban ecosystems research joins mainstream ecology. *Nature*, 467(7312), 153-154.
- McKinney, M.L. (2010) Urbanization, biodiversity, and conservation. *BioScience* 52: 883-890
- Naoroji R. (2011). *Birds of prey of the Indian Subcontinent*. Om Books International, ISBN: 978-8-1871-0769-9, 1-692.
- Newton, I. (2008). The migration ecology of birds—Academic Press.
- Ninan, K. N. (2009). Biodiversity ecosystem services and human well-being. *Conserving and Valuing Ecosystem Services and Biodiversity: Economic, Institutional and Social Challenges*. Earthscan, London, UK, 1-22.
- Pickett, S. T., Cadenasso, M. L., Grove, J. M., Nilon, C. H., Pouyat, R. V., Zipperer, W. C., & Costanza, R. (2001). Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Annual review of ecology and systematics*, 32(1), 127-157.
- 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, Equinox Publishing Ltd, Bristol, CT, USA.

- Prakash, V., Pain, D. J., Cunningham, A. A., Donald, P. F., Prakash, N., Verma, A., & Rahmani, A. R. (2003). Catastrophic collapse of Indian white-backed *Gyps bengalensis* and long-billed *Gyps indicus* vulture populations. *Biological conservation*, 109(3), 381-390.
- Sharan, A. (2014). In the City, Out of Place: Nuisance, Pollution, and Dwelling in Delhi, C. 1850-2000. *OUP Catalogue*.
- Statistics, B. A. H. 19th Livestock census (2012). *Department of Animal Husbandry, Dairying and Fisheries, Ministry of Agriculture. Government of India*.
- Tryjanowski, P., Sparks, T. H., Kuźniak, S., Czechowski, P., & Jerzak, L. (2013). Bird migration advances more strongly in urban environments. *PLoS One*, 8(5), e63482.
- United Nations, Department of Economic and Social Affairs, Population Division (2014). *World Urbanization Prospects: The 2013 Revision*, (ST/ESA/SER.A/366)
- van Dooren, T. (2010). Pain of extinction: The death of a vulture. *Cultural Studies Review*, 16(2), 271-89.

Chapter 1

Density, laying date, breeding success and diet of Black Kites *Milvus migrans govinda* in the city of Delhi (India)

Nishant Kumar, Dhananjai Mohan, Yadvendradev V. Jhala, Qamar Qureshi, Fabrizio Sergio

*Originally published on January 17, 2014; Volume 52, **Bird Study**.*

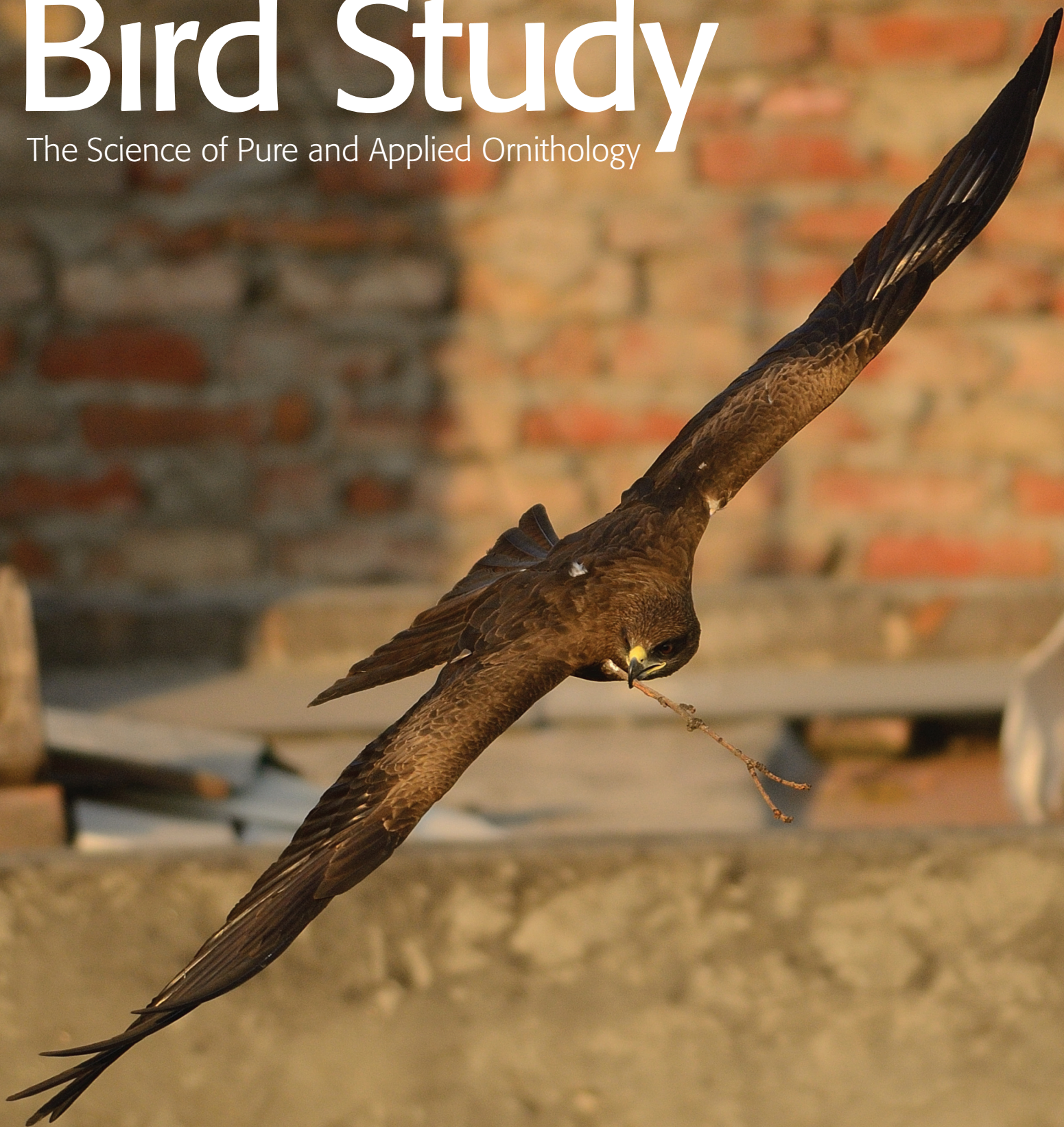
The chapter has been updated with data collected during 2013-2018.

Volume 61, Part 1, February 2014

ISSN: 0006-3657

Bird Study

The Science of Pure and Applied Ornithology



Abstract

At 16.67 nests/km², the breeding density of Black Kites in Delhi (2013- 2015), India, arguably represents the highest concentration of a medium sized raptor recorded in the world (Galushin, 1971). This study aimed to estimate the density, phenology, breeding success and diet of Black Kites in Delhi through a network of 28 sample plots of 1km² distributed throughout the city. A sample of more than 150 nests was checked regularly to record laying date, breeding success and diet and other nesting ecology parameters. These data were collected to test the hypothesis that Black Kites nesting across these sample plots face marked variation in terms of opportunities and challenges, and this would be reflected in their breeding performance. The surveys done through 2013-2015 found average density estimates to be 16.67 ± 7.9 nests/km², comparable to previous studies values, and ranging from 0 nests/km² to 118 nests/km² across the sampling plots. The majority of nests were on trees and the rest on electric pylons and telephone towers. Mean laying period was late January- early February each year and the laying season was protracted over the five winter-spring months (December – April). The mean number of fledged young was 0.62, 0.89 and 1.33 per territorial (n = 780, from 2013- 18), breeding and successful pair respectively. Diet was dominated by scavenged meat and by rats, pigeons and doves abundant in the city. This stability in kite density is probably promoted by a combination of (i) availability of rubbish, (ii) few predators and (iii) high tolerance by people. The conservation status of this raptor seems satisfactory, but removal of mature trees for rapid development may result in local declines or re-distributions, suggesting the need for continued monitoring.

1.1. Introduction

The Black Kite *Milvus migrans* is a medium-sized raptor, currently considered as one of the most numerous and successful birds of prey of the world (Ferguson-Lees & Christie, 2001). It is a generalist, opportunistic feeder, capable of reaching extremely high densities where food concentrations allow it (e.g. review in Malhotra, 2007; Sergio et al., 2005) and may occupy habitats which range from fully natural to completely urban (Ferguson-Lees & Christie, 2001; Ortlieb, 1998). Such adaptability allows it to exploit human-modified habitats, affording the Black Kite, a generally favourable conservation status, with frequent reports of recently increasing populations, despite some local declines (e.g. Bijlsma, 1997; Sergio et al., 2003; Thiollay & Bretagnolle, 2004). This capability to adapt to human landscapes reaches its extreme in populations that nest in fully urban conditions, as frequently observed in Asia and Africa (e.g. Ali & Ripley, 1983; Brown et al., 1982; Desai & Malhotra, 1979; Naoroji, 2006). In these settings, kites are reported not only to use the urban ecosystem for nesting but also for feeding on human offal, road kills, animal carcasses and rubbish, sometimes forming spectacular concentrations of thousands of individuals at rubbish dumps of large cities (Brown et al., 1982; Malhotra, 2007; Naoroji, 2006; Owino et al., 2004). When these dumps are located in the proximity of airports, the concentration of kites often generates serious management problems because of the risk of collisions with planes (e.g. Owino et al., 2004; Satheesan, 1996). It is remarkable that, despite its overall abundance and frequent proximity to humans, Black Kites have very rarely been studied, except for two or three intensively investigated populations, all of them located in Europe and in non-urban settings (e.g. Blanco, 1997; Sergio et al., 2003, 2011; Viñuela et al., 1994).

In the Indian subcontinent, the *govinda* sub-species is well distributed with dense populations in all the major urban centres (Naoroji, 2006). This has attracted many anecdotal observations, as reported in several issues of the Journal of the Bombay Natural History Society (e.g. Abdulali, 1968; Ali, 1926; Fischer, 1906, 1972; Hanxwell, 1892; Mahabal & Bastawade, 1985; Malhotra, 1991). However, quantitative data for this biogeographic region are extremely scarce and previous studies, all of them conducted in the 1970s, have focused on: (1) a coarse estimation of the size of the overall Delhi population (Galushin, 1971) and (2) data on the breeding ecology of the high-density colony of the Delhi Zoo (Desai & Malhotra, 1979). Here, I report comprehensive quantitative data on the density, nest spacing, phenology, breeding success and diet of a fully urban population located within Delhi, India. I then compare the current estimates with historical records and with studies on other kite subspecies.

1.2. Materials and Methods

Study Area

This study builds on work previously undertaken while I was a M.Sc. student at the Wildlife Institute of India, Dehradun. It began at 24 sampling units of 1 km², the area which is regularly monitored each year to document annual variations while each year eight to ten new sampling units are added in the survey scheme. These new plots are monitored only for one year with an aim to have 50-60 plot based uniform coverage for 1500 km² of Delhi by the end of the field work. In each such plot, whose pseudo-replicated number now totals to 79, Black Kites were surveyed through the period 2013 - 2018 (details below, see Appendix). Delhi is a mega-city of 16 million inhabitants in constant, rapid expansion (Census organization of India, 2011). The overall city comprises both urban and semi-urban areas under poor solid waste management,

which affords plenty of food to Black Kites in the form of rubbish, carrion and remains from slaughterhouses.

The climate is semi-arid, with a mean annual precipitation of 64 cm, mainly concentrated in July and August. Temperature ranges from a mean maximum of 39.6° C to a minimum of less than 8.2° C in the winter (<http://amssdelhi.gov.in/climatology/sfd1.htm>). The vegetation of the general region falls within the “northern tropical thorn forest” category (Champion & Seth, 1968).

Field Procedures

Because many areas of the city were private properties not accessible to the public, it was impossible to design a very large continuous study area. Also, because Black Kites in the area can attain extremely high densities, a large number of small plots distributed over a wide area were judged to be better suited to sample all available conditions than a single continuous plot of necessarily limited extension. Therefore, a network of 28 sample plots was designed, each one of approximately 1 km², of homogenous accessibility and distributed throughout the city to cover all types of potential nesting habitats. However, a standardized shape or a standardized surface of 1 km² could not be obtained for all plots because of constraints imposed by private properties and logistical difficulties of access. Private properties had similar landscape features to the surrounding areas of the city and I am confident that their exclusion did not bias the density estimates. However, because of the above, nests which were located at the periphery of each sample plot were not employed to generate estimates of nest spacing (nearest neighbour distance, henceforth referred as NND), unless a complete nest census had been conducted also for the area bordering the quadrat.

I surveyed each quadrat repeatedly every few weeks, starting from the pre-incubation period, by walking slowly and carefully inspecting all potential nest structures (trees, buildings, towers etc.). Structures were classified as active nests when a kite individual or pair was repeatedly observed to perch in the nest or its immediate surroundings, or to add material to the nest. Once found, nests were checked by climbing to them, observing them from nearby vantage points, or through an eight-meter telescopic rod equipped with a video-recording camera. Nests were checked approximately every eight days. However, because of time, safety, accessibility and manpower limitations, data on breeding success could not be collected at all nests.

A nest was classified as depredated if I found remains of plucked chicks. Cases of brood reduction (death of one chick, often caused by its siblings, subsequently fed to other nestlings) were not classified as predation events. Hatching date was calculated by backdating from feather development of nestlings first observed when < 15 days old and in comparison with reference information in Desai & Malhotra (1977), Cramp & Simmons (1980), Hiraldo et al. (1990) and personal data by one of the supervisors (FS). Laying date was estimated by subtracting 30 d, the average incubation period (Viñuela, 1997), from hatching date. During each visit, I collected prey remains found inside and under nests and identified them to the genus or species level assuming the smallest possible number of individuals. These items were used to estimate each prey percentage contribution by number or by mass to the diet of Black Kites.

Following Steenhof (1987): a territorial pair was one that built a nest irrespective of whether it then laid a clutch; a breeding or reproductive pair was one which laid eggs; a successful pair was one which raised at least one nestling until it was 40 days old (the chicks fledge when they are 50 days old); and breeding success was the percentage of successful territorial pairs. There was no need to correct the estimates of breeding success through

Mayfield estimators, because all plots were surveyed repeatedly since pre-lay, and because nests were easy to find and were checked very frequently (approximately every eight days). Density was calculated as the number of territorial pairs per unit area and expressed as the number of pairs/km². The difference in breeding success between nests located in trees and nests built on artificial structures was tested by means of a Z-test (Zar, 1984). Throughout, means are given $\pm$ 1 SE, tests are two-tailed, and statistical significance was set at $\alpha \leq 0.05$.

1.3. Results

Cumulatively, I censused 632 Black Kite nests through 2013 – 2015. Out of these, 595 (94.1%) were located on trees and 37 on artificial structures (electricity pylons and telephone metal towers). Overall, out of the 595 tree nests, 27.9 % were built on *Eucalyptus* spp., 25.6 % on *Ficus* spp., 9.8% on Neem (*Azadiracta indica*), 9.2 % on Vilayati Keekar (*Prosopis juliflora*), 9.1 % on Jamun (*Syzygium cumini*) and 18.5% on other tree species such as *Alstonia scholaris*, *Bombax ceiba*, *Dalbergia sisoo* etc (Fig.1.) The mean nest density was 16.67 ± 7.9 pairs/km² and varied between 0 and 118.3 nests / km² (n = 28 plots). Mean nearest neighbour distance for the sampling done in 2013 was 133 ± 15 m and ranged between 5 and 2315 m (n = 207 pairs).

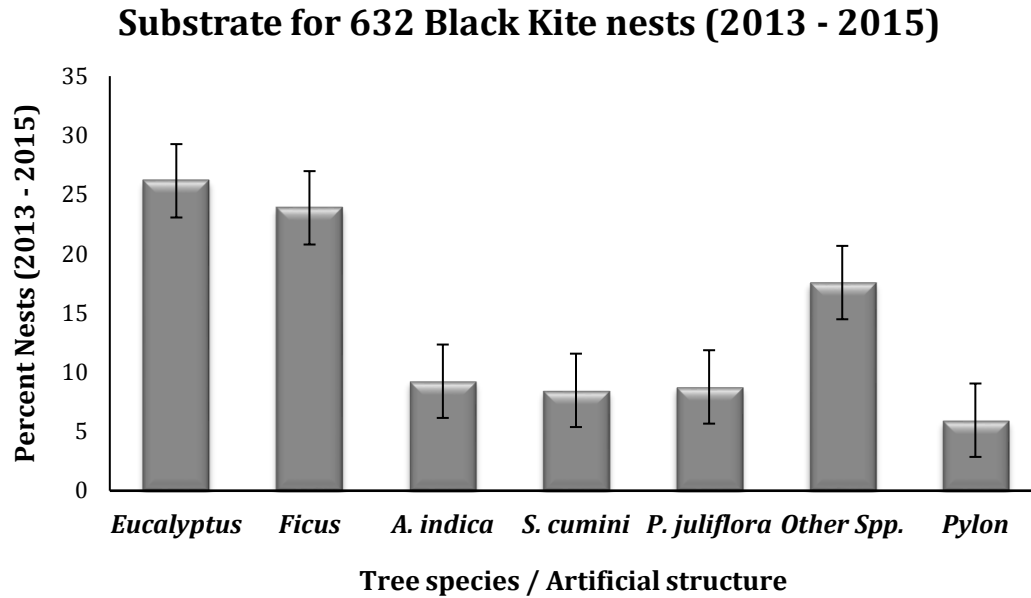


Fig.1. The percent usage of trees and pylons as nesting substrate by the Black Kite population of Delhi (India) in 2013 - 2015 (n = 632).

During 2013-2018, a sample of 780 nests was closely monitored for breeding success. The overall mean laying date was 2nd February (n= 521, SE = 2 days; range 12 December -13 April) and the laying season lasted almost four months each year, with a pronounced peak between the second half of January and first half of February (Fig. 2), a pattern repeated in 2014 and 2015. For a subsample of 151 nests in 2013, when mean monthly temperature and rainfall were superimposed on the laying frequency (Fig. 3), kites seemed to concentrate clutch initiation before the temperatures became excessively high and before the start of the Monsoon rains in June-July. The percentage of clutches initiated each month in 2013 was negatively related to the minimum monthly temperature (linear regression: $B = -1.37 \pm 0.35$; B for constant = 34.21 ± 7.14 ; n = 12; Bonferroni-corrected P = 0.006; $R^2 = 0.56$) and quadratically related to the maximum monthly temperature (quadratic regression: B for linear term = -11.86 ± 3.66 ; Bonferroni-corrected P = 0.02; B for quadratic term: = 0.17 ± 0.06 ; Bonferroni-corrected P =

0.02; B for constant = 211.37 ± 54.04 ; $n = 12$; $R^2 = 0.77$), while egg laying stopped with the commencement of the rains and was initiated again only after the monsoon season. Finally, the number of young fledged by each pair declined with laying date (linear regression: $B = -0.13 \pm 0.03$; B for constant = 1.66 ± 1.77 ; $n = 65$, $P = 0.001$; $R^2 = 0.17$).

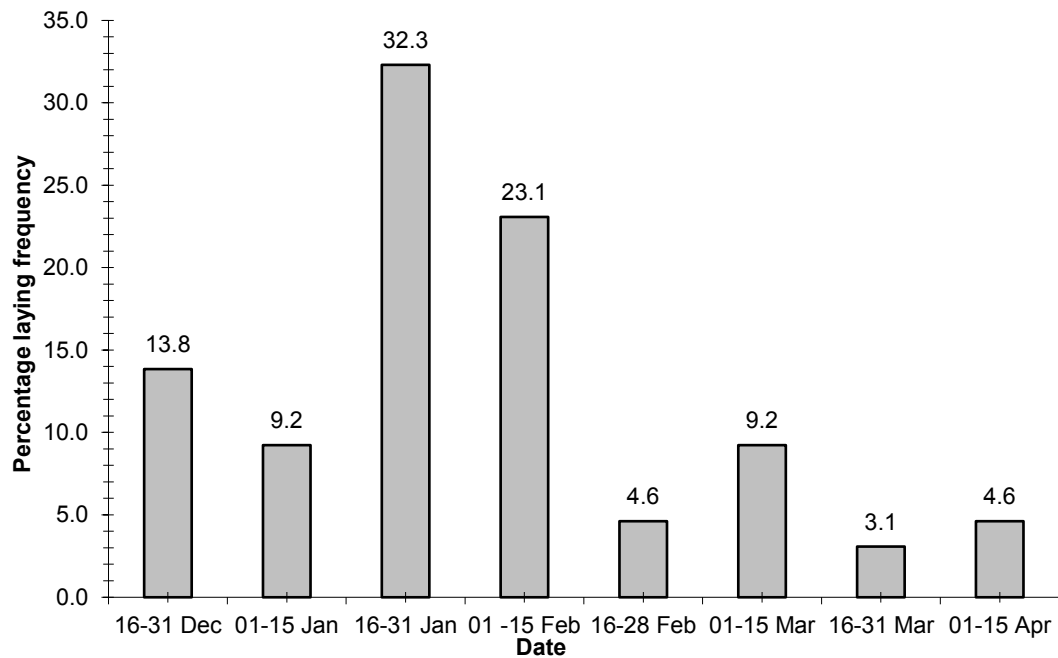


Fig. 2. Temporal frequency of laying dates in the Black Kite population of Delhi (India) in 2013 ($n = 65$).

Mean clutch size for 2013 – 2018 was 2.13 ± 0.06 ($n = 521$). Mean hatching success was $84 \pm 2.2\%$ ($n = 521$ nests). The mean percentage of nestlings lost by brood reduction during 2013-18 was 0.28 ± 4.48 per brood ($n = 568$ nests). The mean number of fledged young during 2013 -18 was 0.62 per territorial pair ($n = 780$), 0.89 per breeding pair ($n = 521$) and 1.33 per successful pair ($n = 308$). In 2013, forty-eight percent of territorial pairs successfully raised their nestlings to fledging age ($n = 151$). This value was 55.52 % for 2014 and 39.2% for the 2015

monitoring. Cumulatively, the overall breeding success for a sample of 780 nests (2013- 2018) was 39.49%. For the sampling in 2013, there was a trend for breeding success to be higher for nests on trees than for nest on the artificial structures (46 % vs. 27.8 %; $Z = 1.8$, $P = 0.07$, n for tree-nests = 130, n for artificial substrate = 21).

3.1 *Diet*

Kite diet included all vertebrate classes but was strongly dominated, both by mass and number, by three main items: (1) remains from slaughterhouses, mainly in the form of compact chunks of meat; (2) rats; and (3) medium-sized urban birds, such as doves and pigeons (Table 1).

Table 1. Diet of breeding Black Kites in Delhi, India (2012-13), as estimated by food remains collected inside and under the nest.

Prey category	Frequency by number (%)	Frequency by mass (%)
Fish ^a	0.8	1.0
Amphibians ^b	0.7	0.7
Reptiles ^c	0.7	0.3
Birds	24.6	31.9
i) Rock Pigeon (<i>Columba livia</i>)	13.1	16.2
ii) Collared Dove (<i>Streptopelia decaocto</i>)	4.1	3.3
iii) Other birds ^d	7.4	12.4
Mammals ^e	9.8	20.2
Scavenged meat ^f	63.4	45.9
i) Meat Scraps	47.1	35.6
ii) Domestic chicken	11.5	6.1
iii) Cattle ^g	4.1	3.5
iv) Fish ^h	0.7	0.7

^a Includes: unidentified fish (n=1)

^b Includes: Indian bullfrog (n = 1).

^c Includes: Common house gecko (n = 1).

^d Includes: Moorhen (*Gallinula chloropus*) (n= 1), Indian Roller (*Coracias benghalensis*) (n= 1), Unidentified birds (n=7)

^e Mammals which were unlikely to be consumed as carrion. Includes: Norway rat (*Rattus norvegicus*) (n = 11) and Palm squirrel (*Funambulus pennantii*) (n = 1)

^f Includes prey items that were considered to have been collected as carrion from local rubbish dumps and slaughterhouses.

^g Includes: Buffalo (n=2), Goat (n=3).

^h Includes: Large unidentified fish skin, likely from fish market.

1.4. Discussion

The study confirms that Black Kites have maintained extremely high breeding densities throughout the city of Delhi, as already observed in the 1970s (Galushin, 1971). When compared with data from other populations (reviewed in Table 2), the density observed in the urban environment of Delhi was higher than any previously published estimate. This is then, probably, the highest density ever recorded over a large, continuous area for any bird of prey of this size. The capability to attain such a high population-level over such a large region is likely to be promoted by a combination of at least three factors. (1) First, the rubbish management plans of such a rapidly developing mega-city are inevitably poor, which results in a network of enormous, legally-authorized rubbish dumps coupled with hundreds of smaller, and often illegal sites where garbage is dumped daily. At an even finer-scale, private individuals, families and shops often leave their daily garbage directly in the streets, resulting in a network of ephemeral, small piles of food. In turn, these must promote large populations of potential prey species, such as rats and pigeons. All the above, coupled with the high abundance of meat and fish shops throughout the city, sets an ideal scenario of enormous food availability for an opportunistic predator and facultative scavenger. (2) Second, the attitudes of local people towards kites, and wildlife in general, are extremely positive and tolerant, even despite the fact that some kites can be very aggressive in defending their nest against nearby passers-by. I am not aware of any cases of persecution of kites in Delhi, which is confirmed by the relative absence of fear of humans shown by most kites in comparison to European conspecifics. (3) Third, the city provides an environment with a low abundance of potential predators. The only potential nest predators known to occur locally are Indian Eagle Owls *Bubo bubo bengalensis*, House Crows *Corvus splendens* and Rhesus Macaques *Macaca mulatta*. The latter two species can be locally

abundant, but are often deterred by the very aggressive and effective nest defence behaviour of parent kites.

When compared to historical records, the high density record seemed remarkably stable over several decades. However, rapid city-wide surveys and data from the New Delhi Zoological Park suggested much higher current densities than had been observed previously (Desai & Malhotra, 1979; Galushin, 1971; see Table 2). This likely resulted from the enormous changes in the city's dimensions, population size and management, although, the overall density of the NZP area (3 km² area which included 40 acre of NZP) remained stable. In a way, the differential sectoral development in the city tends to do both, support or reduce kite density, depending upon local development and juxtaposition of favourable habitat patches and food resources. Such positive overall status is in place despite the recent, virtual extinction of the locally abundant populations of a potential trophic competitor, the White-rumped Vulture *Gyps bengalensis*, the former primary scavenger (Naoroji, 2006; Prakash et al., 2003). The kite population thus seemed very resilient to change in terms of overall density.

Table 2. Breeding density and nest spacing of Black Kite populations in Europe and India (Delhi), 1966-2015. Density was expressed as territorial pairs/10 km² for clarity of presentation. The 2013 - 15 data from the current study are presented twice in the table: (i) for the whole study area, i.e. representative of the whole Delhi population; and (b) for the high-density sector of the New Delhi National Zoological Park (NZN), in order to make them comparable to historical data from the 1970s by Malhotra (2007).

Area (period)	Habitat	Density (per/10 km ²) (n)	Nearest neighbour distance in meters (n)
Delhi, India (2015) ¹⁷	U	170 (231)	-
NZN, India (2015) ¹⁷	U	1093 (70)	-
Delhi, India (2014) ¹⁷	U	183 (157)	-
NZN, India (2014) ¹⁷	U	1183 (71)	-
Delhi, India (2013) ¹⁷	U	150 (244)	133 (207)
Delhi, India (1967-1969) ³	U	161 (~560)	-
NZN, India (1979) ¹⁶	U	250 (18-21)	-
NZN, India (2013) ¹⁷	U	870 (70)	-
Matas Gordas, Spain (1987-1989) ¹⁰	M	70-150 (21-45)	-
Matas Gordas, Spain (1992-2000) ¹⁵	M	100.8 (515)	-
Doñana, Spain (1981-1984) ⁸	M	26.7 (80)	206 (47) ^a
RBD, Spain (1989–2000) ¹⁵	M	15.1 (1059)	-
Lac Lemman, Switzerland (1975-1990) ¹¹	F	10.1 (319)	-
Neuchatel, Switzerland (1968) ⁵	FL	7.1 (337)	-
Lorraine, France (1966) ¹	WP	4.5 (66)	-
Rhône Plain, France (1970) ⁵	RP	60.9 (140)	-
Limousin, France (1976-1978) ⁴	PW	1.0 (21)	-
Lake Lugano, Italy (1992-1996) ¹³	WL	2.4-3.8 (27-41)	441 (175)
Lake Lugano, Italy (1992–2003) ¹⁵	WL	2.9 (365)	-
Lake Maggiore, Italy (1996–2000) ¹⁴	WL	- (24)	-

Lake Como, Italy (1996–2000) ¹⁴	WL	4.7 (40)	-
Lake Iseo, Italy (1996–2000) ¹⁴	WL	3.5 (48)	-
Lake Idro, Italy (1997–2001) ¹⁴	WL	6.7 (37)	-
Lake Garda, Italy (1997–2000) ¹⁴	WL	1.5 (18)	-
Sarca Valley, Italy (1997–2003) ¹⁴	WL	1.3 (88)	-
Castelporziano, Italy (1991-1992) ⁹	WF	3.3 (16)	103 (16) ^b
Monti della Tolfa, Italy (1973-1980) ⁷	WP	0.5 (42)	-
Costance Lake, Germany (1968-1969) ²	FL	1.9-2.2 (25-30)	-
Drömling, Germany (1993-1994) ¹²	F	0.7 (8)	2330 (8) ^c
Brandenburg, Germany (1979) ⁶	F	0.7 (215)	-

^a Estimate from Bustamante & Hiraldo (1990), for the period 1985-1988.

^b Refers to a single colony.

^c Calculated from the published map.

U: Urban, M: Marshland, FL: Farmland & Lake, WL: Woodland & Lake, F: Farmland, WP: Woodland & Pasture, WF: Woodland & Farmland, FL: Farmland & Lake, PW: Pasture & Woodland, RP: River Plain

¹Thiollay 1967, ²Heckenroth 1970, ³Galushin 1971, ⁴Nore 1979, ⁵Sermet 1980, ⁶Fiuczynski 1981,

⁷Petretti & Petretti 1981, ⁸Hiraldo *et al.* 1990, ⁹De Giacomo *et al.* 1993, ¹⁰Viñuela *et al.* 1994,

¹¹Henrioux & Henrioux 1995, ¹²Seelig *et al.* 1996, ¹³Sergio & Boto 1999, ¹⁴Sergio *et al.* 2003, ¹⁵Sergio *et al.* 2005, ¹⁶Malhotra 2007, ¹⁷This study

The laying season was protracted over almost four months, probably as a result of the long period of warm, favourable weather and of the stable food supply provided by the urban environment (Fig. 3). The temporal peak and range of laying dates seemed to be arranged so that most nestlings fledged well before the high temperatures and the marked peak in precipitation caused by Monsoon rains in July-August (Fig. 3). The negative effect of high temperatures and rainfall on kite foraging performance, egg viability and breeding success has been reported for various European populations (Hiraldo *et al.*, 1990; Sergio, 2003; Viñuela, 2000). The observed, lengthy range of laying dates compares to a duration of the laying season of 28 days for kite populations of the Italian Alps and to 2.8 months for the population of Doñana

National Park, in the extreme south of Europe (F. Sergio, pers. data). This suggests a North-South latitudinal gradient in the length of kite breeding seasons. Protracted breeding seasons are increasingly reported as progressively more studies of birds of prey are conducted in tropical or more southern latitudes (e.g. Ogada & Kibuthu, 2012; Simmons, 2000).

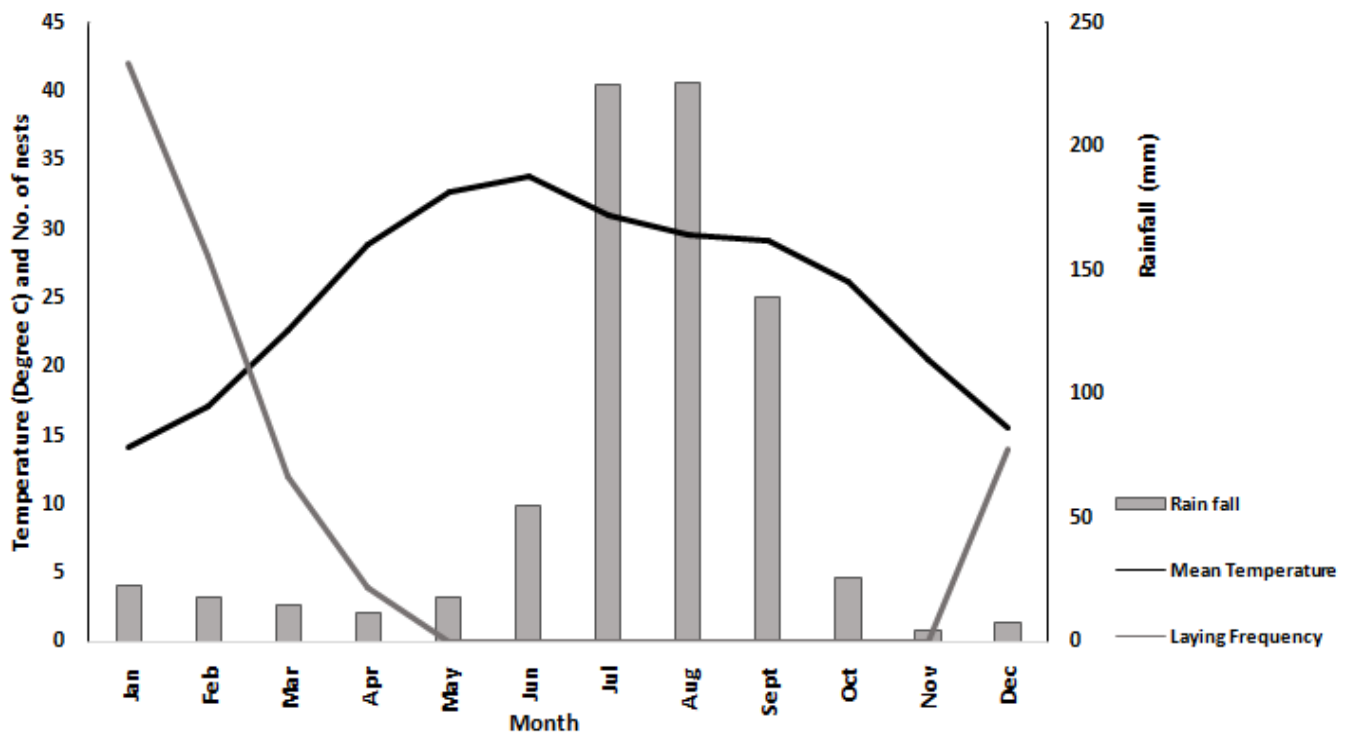


Fig.3. Mean temperature, monthly rainfall and Black Kite laying frequency in 2013 in Delhi (data from: <http://amssdelhi.gov.in/climatology/sfd1.htm>).

When compared to other populations (review in Table 3), my estimates of breeding success were lower than in other studies and this may be a consequence of density-dependent processes in a crowded, saturated population (e.g. Newton, 1998). The fact that similarly low levels of reproduction were reported for another saturated population (Doñana, Sergio et al., 2011) lends support to this impression (Fig. 4). However, in the absence of more information, other alternative explanations cannot be discounted: for example, it is not known whether a diet based

largely on rubbish and meat produced for human consumption could spread pathogens or toxic substances among the offspring. In addition to this, I observed considerable loss of chicks during the 2015 season to avian pox, a disease which only affects the nest bound offsprings. Nine out of 10 nests, with fledglings having cases of avian pox (late April 2015) in NZP, suffered eventual failure. This was likely caused by the heavy and abrupt downpour in March 2015 which increased the population of insect vectors of the disease (Unpublished, camera trap data).

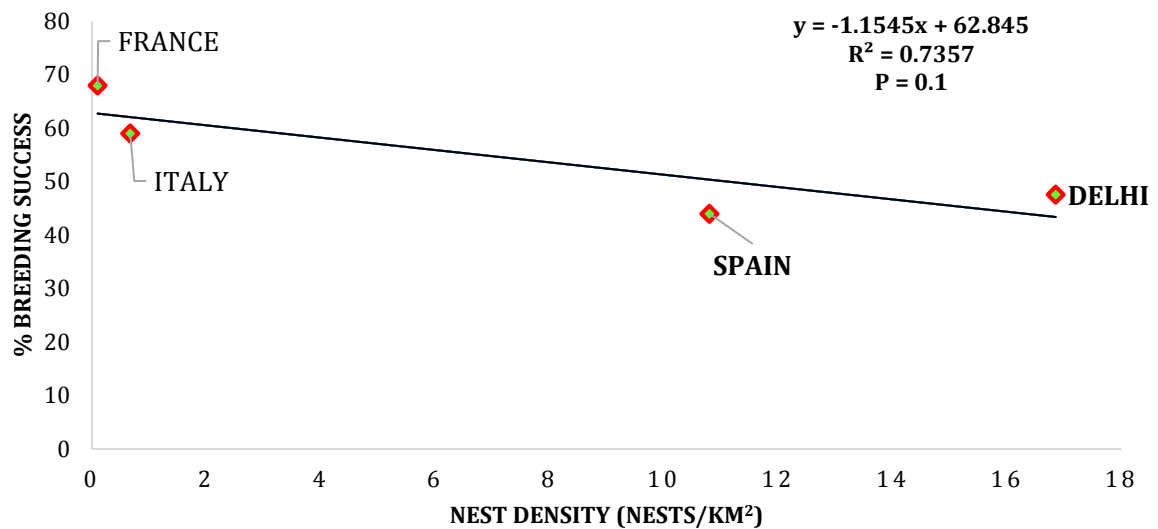


Fig.4. The relationship between the nest density of Black Kite populations in Asia and Europe, and the **mean breeding success** over several years.

Table 3 Productivity of Black kite populations in Europe and Asia, 1966-2015. The 2013 -18 data from the current study are presented twice in the table: (i) for the whole study area, i.e. representative of the whole Delhi population; and (ii) for the high-density sector of the New Delhi National Zoological Park (NZP), in order to make them comparable to historical data from the 1970s by Desai & Malhotra (1979).

Area (period)	Habitat (n)	Clutch size	Hatching success ^a (eggs)	Breeding success	Mean number of fledged young		
					territorial pair	breeding pair	successful pair
Delhi, India (2013-2018) ¹¹	U (780)	2.13(521) ^b	84% (521) ^b	39.49%	0.62	0.89(521) ^b	1.33 (308) ^b
Delhi, India (2015) ¹¹	U (212)	2.14 (193)	65.9 % (106) ^b	39.2%	-	-	-
Delhi, India (2014) ¹¹	U (157)	-	-	55.5%	-	-	-
Delhi, India (2013) ¹¹	U (151)	2.09(100) ^b	68% (157) ^b	48%	0.73	1.09(100) ^b	1.52 (72) ^b
NZP, India (1973-1976) ²	U (45)	2.3 (60) ^b	55% (102) ^b	-	0.98	-	-
NZP Park, India (2013) ¹¹	U(46)	2.04 (36)	62% (55) ^b	59%	0.78	0.95 (38) ^b	1.44 (25) ^b
RBD, Spain (1989–2000) ¹⁰	WL(1059)	2.02	67.4 % (416)	41%	0.59	0.71	1.43
Matas Gordas, Spain (1992–2000) ¹⁰	GM(515)	2.12	70.3 % (232)	44%	0.61	0.85	1.46
Germany (1992-1995) ^{7c}	-(599)	-	-	79%	1.63	-	2.07 (471) ^b
Limousin, France (1976-1978) ³	PW (22)	-	-	68%	-	1.32	1.93 (15) ^b
Berlin, Germany (1940-1979) ⁴	F (215)	-	-	62%	1.20		1.90 (133) ^b
Lake Lugano, Italy (1992-1996) ⁹	WL (143)	2.29 (42) ^b	84% (96) ^b	55%	0.97	1.1 (95) ^b	1.78 (78) ^b
Lake Lugano, Italy (1992–2003) ¹⁰	WL (315)	2.3	74 % (88)	50%	0.90	1.24	1.80

Lake Maggiore, Italy (1996–2000) ¹⁰	WL (30)	-	-	50%	0.87	-	1.73
Lake Como, Italy (1996–2000) ¹⁰	WL (40)	-	-	48%	0.75	-	1.58
Lake Iseo, Italy (1996–2000) ¹⁰	WL (48)	-	-	38%	0.48	-	1.10
Lake Idro, Italy (1997–2001) ¹⁰	WL (37)	-	-	59%	1.05	-	1.63
Lake Garda, Italy (1997–2000) ¹⁰	WL (18)	-	-	44%	0.83	-	2.14
Sarca Valley, Italy (1997–2003) ¹⁰	WL (88)	-	-	40%	0.63	-	1.62
Slovakia (1975-1989) ⁵	- (162)	2.98 (44) ^b	-	-	-	2.31	-
Lac Lemán, Switzerland (1975-1990) ⁸	FL (165)	2.25	-	-	-	2.02	-
Lorraine, France (1966) ¹	WP (66)	2.26 (45) ^b	-	-	1.32	1.58 (55) ^b	-
Nagasaki, Japan (1983-1986) ⁶	FP (32)	2.18 (28) ^b	79% (61) ^b	75%	1.00	1.14 (28) ^b	1.33 (24) ^b

^a Data on hatching success not shown in table: 75% ($N = 36$ eggs from 14 nests, Hakel, Germany, 1957; Stubbe 1961) and 64% ($N = 28$ eggs from 10 nests, Lazio, Italy, date unknown; Petretti 1992).

^b Sample size (when different from that in column “Habitat (n)”).

^c Data also from Mammen & Stubbe (1995, 1996)

U: Urban, GM: Grassland & Marshland, FL: Farmland & Lake, WL: Woodland & Lake, F: Farmland, WP: Woodland & Pasture, FL: Farmland & Lake, PW: Pasture & Woodland, FP: Fishing Port

¹Thiollay 1967, ²Desai & Malhotra 1979, ³Nore 1979, ⁴Fiuczynski 1981, ⁵Danko 1989, ⁶Koga et al. 1989, ⁷Gedeon 1994^c, ⁸Henrioux & Henrioux 1995, ⁹Sergio & Boto 1999, ¹⁰Sergio et al. 2005, ¹¹This study

Finally, the observed diet composition confirmed the full dependence of the local kite population on urban resources, such as meat scraps from slaughterhouses or prey species which were extremely abundant within the city, such as rats, feral pigeons and wild dove species. The current picture of the diet does not suggest that kites range frequently, if at all, out of the city to capture wild prey in surrounding rural areas. This confirms that the high density attained within the urban setting is promoted by attraction to a dense food source. Regarding the estimates of various prey components of the breeding kites' diet (Table 1), it must be noted that representation of boneless meat chunks are unlikely to be justified by opportunistic sampling of prey remains. Therefore, our estimates must be treated as cursory, with scope of improvement by deployment of trail cameras which can monitor nest activities 24 x 7 (see Chapter 5). Use of cameras would address the likelihood of bias in context of meat chunks, which did not leave any remains for us to factor in the diet analyses.

In summary, extensive foraging opportunities, a stable favourable climate, absence of human persecution and low density of potential predators have probably contributed to one of the densest raptor populations of the world. The current conservation status of the studied population seems satisfactory, but recent urban development is causing extreme and almost complete removal of mature trees in some sectors of the city. In turn, this could limit the kite population in the future, or trigger local declines and re-distributions, especially when considering that artificial structures do not seem to fully compensate for the absence of trees (Fig. 1, Chapter 5). Thus, given the abundance of the species and the current urban sanitary levels, the ecological service provided by kites through removal of organic rubbish must be valuable, suggesting the need for ecologically sensitive urban planning of the remaining green

areas. This calls for the importance of continued monitoring of the population and its nesting requirements in future years.

References

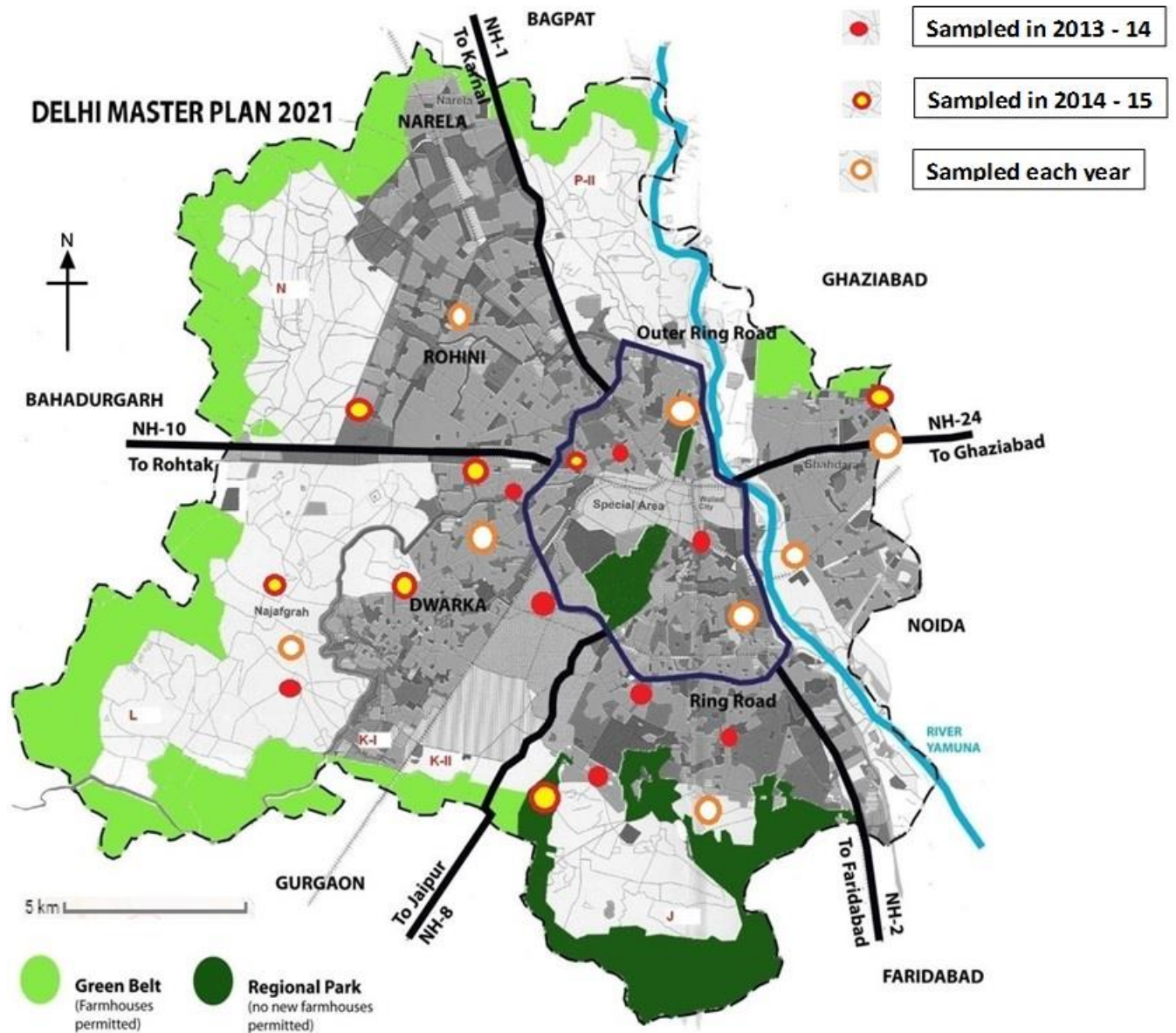
- Abdulali, H., & Nair, J. G. (1968). Extension of the range of the large Indian Kite *Milvus migrans lineatus* (Gray). *J. Bombay Nat. History Soc*, 65, 774.
- Abdulali, H. (1972). Some bird notes by WF Sinclair. *J. Bombay Nat. History Soc*, 69, 422-424.
- Ali, S., & Ripley, D.A. (1983). No. 132. Black Kite (*Milvus migrans migrans*) (Boddaert), *Handbook of the Birds of India and Pakistan*. Oxford University Press, New Delhi, Volume 1 (Divers to Hawks) 226.
- Ali, S. (1926). Mating habits of common Pariah Kite (*Milvus migrans govinda*). *J. Bombay Natl. Hist. Soc*, 31, 524-526.
- Baccetti, N. (Eds.) (1992). *Fauna d'Italia*. Edizioni Calderini, Bologna, Italy.
- Bijlsma, R.G. (1997). Black Kite. In *The EBCC Atlas of European breeding birds, their distribution and abundance*, eds. W.J.M. Hagemeijer, & M.J. Blair, M. J, 132-133. T & AD Poyser, London.
- Blanco, G. (1997). Role of refuse as food for migrant, floater and breeding Black Kites (*Milvus migrans*). *Journal of Raptor Research*, 31, 71-76.
- Brown, L. H., Urban, E. K., & Newman, K. (1982). *The Birds of Africa*, Vol. 1. London. Academic Press, London.
- Bustamante, J., & Hiraldo, F. (1990). Adoptions of fledglings by black and red kites. *Animal behaviour*, 39, 804-806.
- Census Organization of India. (2011). Census of India. Available from: <http://censusindia.gov.in/2011census> [accessed 27 September 2015]
- Champion, S. H., & Seth, S. K. (1968). A revised survey of the forest types of India. *Manager of Publications*, Government of India, New Delhi.
- Cramp, S., & Simmons, K. E. L. (1980). *Handbook of the birds of Europe, the Middle East and North Africa*. Vol. 2. Hawks and bustards. Oxford Univ. Press, Oxford, U.K.

- Danko, Š. (1989). Five young in the nest of a Black Kite (*Milvus migrans*). *Buteo*, 4, 87-92.
- De Giacomo, U., Martucci, O., & Tinelli, A. (1993). L'alimentazione del Nibbio bruno (*Milvus migrans*) nella Tenuta di Castelporziano (Roma). *Avocetta*, 17, 73-78.
- Desai, J. H., & Malhotra, A. K. (1979). Breeding biology of the pariah kite *Milvus migrans* at Delhi zoological park. *Ibis*, 121(3), 320-325.
- Ferguson-Lees, J., & Christie, D. A. (2001). Monk vulture: *Aegypius monachus*. *Raptors of the World*, 437-438.
- Fischer, C. E. C. (1906). Flocking of Kites. *Journal of the Bombay Natural History Society*, 17(2), 525 - 526.
- Fiuczynski, D. (1981). Berliner milan-chronik (*Milvus migrans* and *Milvus milvus*). *Beitr. Vogelk*, 27, 161-196.
- Galushin, V. M. (1971). A huge urban population of birds of prey in Delhi India. *Ibis*, 113(4), 522-522.
- Gedeon, K. (1994). *Monitoring Greifvögel und Eulen: Grundlagen und Möglichkeiten einer langfristigen Überwachung von Bestandsgrößen und Reproduktionsdaten*. Martin-Luther-Universität.
- Hanxwell, T. A. (1892). Nest and eggs of the Crested Black Kite. *Journal of the Bombay Natural History Society*, 7(3), 403-404.
- Heckenroth, H. (1970). Der Greifvogelbestand des Bodanrücks (Bodensee) 1968 und 1969. *Anz. Orn. Ges. Bayern*, 9, 47-51.
- Hiraldo, F., Veiga, J. P., & Mañez, M. (1990). Growth of nestling black kites *Milvus migrans*: effects of hatching order, weather and season. *Journal of Zoology*, 222(2), 197-214.
- Indian Meteorological Department. (2013). <http://amssdelhi.gov.in/climatology/sfd1.htm>. [Accessed 27 September 2015].

- Koga, K., Siraishi, S., & UCHIDA, T. (1989). Breeding ecology of the Black-eared Kite *Milvus migrans lineatus* in the Nagasaki Peninsula, Kyushu. *Japanese Journal of Ornithology*, 38(2), 57-66.
- Mahabal, A., & Bastawade, D. B. (1985). Population ecology and communal roosting behaviour of pariah kite *Milvus migrans govinda* in Pune (Maharashtra). *Journal of the Bombay Natural History Society. Bombay*, 82(2), 337-346.
- Malhotra, A.K., (1991). Site fidelity and power of recognition in Pariah Kite *Milvus migrans govinda*, *Journal of the Bombay Natural History Society*, 87, 458.
- Malhotra, A.K. (2007). Tiger of sky-Pariah Kite, *PhD thesis*, Shilalekh Publishers, Delhi.
- Mammen, U., & Stubbe, M. (1996). Jahresbericht 1995 zum Monitoring Greifvögel und Eulen Europas. *Jahresbericht zum Monitoring Greifvögel und Eulen Europas*, 8.
- Mammen, U., & Stubbe, V. (1995). Jahresbericht 1994 zum monitoring Greifvögeln und Eulen Europas Jahresber. *Monitoring Greifvögel Eulen Europas*, 7(1), 78.
- Naoroji, R. (2006). Birds of prey of the Indian subcontinent. Christopher Helm.
- Newton, I. (1998). *Population limitation in birds*. Academic press.
- Nore, T. (1979). Rapaces diurnes communs en Limousin pendant la periode de nidification (Buse, Bondre, Milan noir, Busards saint-martin et Cendres). *Alauda*. 47, 183-194.
- Ogada, D. L., & Kibuthu, P. M. (2012). Breeding ecology of Mackinder's Eagle-Owls (*Bubo capensis mackinderi*) in farmlands of central Kenya. *Journal of Raptor Research*, 46(4), 327-335.
- Ortlieb, R. (1998). Der Schwarzmilan. *Die Neue Brehm-Bücherei*, Hohenwarsleben, Germany
- Owino, A., Biwott, N., & Amutete, G. (2004). Bird strike incidents involving Kenya Airways flights at three Kenyan airports, 1991–2001. *African Journal of Ecology*, 42(2), 122-128.
- Peteretti, F. (1992). *Nibbio bruno*. 459-465 in P. Brichetti, P. De Franceschi & N.

- Petretti, A., & Petretti, F. (1981). A population of diurnal raptors in central Italy. *Gerfaut*, 71, 143-156.
- Prakash, V., Pain, D. J., Cunningham, A. A., Donald, P. F., Prakash, N., Verma, A., & Rahmani, A. R. (2003). Catastrophic collapse of Indian white-backed Gyps bengalensis and long-billed Gyps indicus vulture populations. *Biological conservation*, 109(3), 381-390.
- Satheesan, S.M. (1996). Raptors associated with Airports and Aircrafts; *Raptors in Human landscapes*. Academic press limited.
- Seelig, K. J. (1996). *Die Vögel im Naturpark Drömling*. Förderkreis Museum Heineanum.
- Sergio, F., Blas, J., Forero, M., Fernández, N., Donazar, J. A., & Hiraldo, F. (2005). Preservation of wide-ranging top predators by site-protection: black and red kites in Doñana National Park. *Biological Conservation*, 125(1), 11-21.
- Sergio, F., Blas, J., López, L., Tanferna, A., Díaz-Delgado, R., Donazar, J. A., & Hiraldo, F. (2011). Coping with uncertainty: breeding adjustments to an unpredictable environment in an opportunistic raptor. *Oecologia*, 166(1), 79-90.
- Sergio, F., Pedrini, P., & Marchesi, L. (2003). Reconciling the dichotomy between single species and ecosystem conservation: black kites (Milvus migrans) and eutrophication in pre-Alpine lakes. *Biological Conservation*, 110(1), 101-111.
- Sergio, F. (2003). From individual behaviour to population pattern: weather-dependent foraging and breeding performance in black kites. *Animal Behaviour*, 66(6), 1109-1117.
- Sergio, F., & Boto, A. (1999). Nest dispersion, diet, and breeding success of Black Kites (Milvus migrans) in the Italian pre-Alps. *Journal of Raptor Research*, 33, 207-217.
- Sermet, E. 1980. *Milan noir*. Pages 88-89 in Schifferli, A. (1980). *Atlas des oiseaux nicheurs de Suisse*. Schweizerische Vogelwarte Sempach.
- Simmons, R. E., & Simmons, J. R. (2000). *Harriers of the world: their behaviour and ecology* (Vol. 11). Oxford University Press on Demand.

- Steenhof, K. (1987). Assessing raptor reproductive success and productivity. *Raptor management techniques manual*, 157-170.
- Stubbe, C. (1961). Die Besiedlungsdichte eines abgeschlossenen Waldgebietes (Hakel) mit Greifvögeln im Jahre 1957. *Beitr. Vogelkd*, 7, 155-224.
- Thiollay, J.M., & Bretagnolle, V. (2004). Rapaches nicheurs de France: distribution, effectifs et conservation. *Delachaux et Niestlé*, Paris, France.
- Thiollay, J. M. (1967). Ecologie d'une population de rapaces diurnes en Lorraine.
- Viñuela, J., Villafuerte, R., & Court, C. D. L. (1994). Nesting dispersion of a black kite population in relation to location of rabbit warrens. *Canadian Journal of Zoology*, 72(9), 1680-1683.
- Viñuela, J. (1997). Laying order affects incubation duration in the Black Kite (*Milvus migrans*): Counteracting hatching asynchrony? *The Auk*, 192-199.
- Viñuela, J. (2000). Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. *Behav. Ecol. Sociobiol*, 45, 333-343.
- Zar, J. H. (1984). *Bio-statistical analysis*. Englewood Cliffs, NJ: Prentice-Hall, 283.



Appendix: Delhi Master plan map 2021 (source: Municipal Corporation of Delhi), with the sampling units (the larger bi-colour dots depict the sampling units followed each year to monitor annual variations, while the single colour dots represent the sampling units followed only once).

Density, laying date, breeding success and diet of Black Kites *Milvus migrans govinda* in the city of Delhi (India)

NISHANT KUMAR^{1*}, DHANANJAI MOHAN^{1†}, YADVENDRADEV V. JHALA¹, QAMAR QURESHI¹ and FABRIZIO SERGIO²

¹Wildlife Institute of India, Post Box # 18, Chandrabani, Uttarakhand 248001, India; ²Estacion Biologica de Doñana-CSIC, C/ Americo Vespucio, s/n, Sevilla 41092, Spain

Capsule The density of Black Kites in Delhi, India, may represent the highest concentration of a raptor recorded in the world and has not declined since the 1960s.

Aims To estimate the density, phenology, breeding success and diet of Black Kites in Delhi.

Methods During 2013, Black Kite nests were surveyed in 24 plots of 1 km² distributed throughout Delhi. A sample of 151 nests was checked regularly to record laying date, breeding success and diet.

Results The average density was 15 nests/km². The majority of nests were on trees (91%) and the rest on artificial structures. Mean laying date was 31 January and the laying season was protracted over four months. Mean number of fledged young was 0.73, 1.09 and 1.53 per territorial, breeding and successful pair. Diet was dominated by scavenged meat and by rats, pigeons and doves abundant in the city.

Conclusions Density has been stable since 1960–1970s and probably represents the highest ever recorded for a raptor. This is probably promoted by a combination of (i) availability of rubbish, (ii) few predators and (iii) high tolerance by people. The conservation status of this raptor seems satisfactory, but removal of mature trees for rapid development may result in local declines or re-distributions, suggesting the need for continued monitoring.

The Black Kite *Milvus migrans* is a medium-sized raptor, currently considered as one of the most numerous and successful birds of prey of the world (Ferguson-Lees & Christie 2001). It is a generalist, opportunistic feeder, capable of reaching extremely high densities where food concentrations allow it (e.g. review in Sergio *et al.* 2005, Malhotra 2007) and may occupy habitats which range from fully natural to completely urban (Ortlieb 1998, Ferguson-Lees & Christie 2001). Such opportunism and capability to exploit human-modified habitats has afforded this species a generally favourable conservation status, with frequent reports of recently increasing populations, despite some local declines (Bijlsma 1997, Sergio *et al.* 2003, Thiollay & Bretagnolle 2004).

This capability to adapt to human landscapes reaches its extreme in populations that nest in fully urban conditions, as frequently observed in Asia and Africa

(Desai & Malhotra 1979, Brown *et al.* 1982, Ali & Ripley 1983, Naoroji 2006). In these settings, kites are reported to use the urban ecosystem not only for nesting but also for feeding on human offal, road kills, animal carcasses and rubbish, sometimes forming spectacular concentrations of thousands of individuals at rubbish dumps of large cities (Brown *et al.* 1982, Owino *et al.* 2004, Naoroji 2006, Malhotra 2007). When these dumps are located in the proximity of airports, the concentration of kites often generates serious management problems because of the risk of collisions with planes (Satheesan 1996, Owino *et al.* 2004). It is remarkable that, despite their overall abundance and frequent proximity to humans, Black Kites have been very rarely studied, except for two or three intensively investigated populations, all of them located in Europe and in non-urban settings (Viñuela *et al.* 1994, Blanco 1997, Sergio *et al.* 2003, 2011).

In the Indian subcontinent, where we conducted our research, the *govinda* sub-species is well distributed with dense populations in all the major urban centres (Naoroji 2006), which has attracted many anecdotal observations, as reported in several issues of the *Journal*

*Correspondence author. Emails: nishant@wii.gov.in, ryu.nishant@gmail.com

[†]Current address: Office of Chief Wildlife Warden, Uttarakhand Forest Department, Mohabbewala, Dehradun, Uttarakhand 248001, India.

of the Bombay Natural History Society (Hanxwell 1892, Fischer 1906, Ali 1926, Abdulali 1968, 1972, Mahabal & Bastawade 1985, Malhotra 1991). However, quantitative data for this biogeographic region are extremely scarce and previous studies, all of them conducted in the 1970s, have focused on: (1) a coarse estimation of the size of the overall Delhi population (Galushin 1971) and (2) data on the breeding ecology of the high-density colony of the Delhi Zoo (Desai & Malhotra 1979). Here, we report comprehensive quantitative data on the density, nest spacing, phenology, breeding success and diet of a fully urban population located within Delhi, India. We then compare the current estimates with historical records and with studies on other kite sub-species.

METHODS

Study area

Black Kites were surveyed in 2013 in 24 plots (details below) within an overall area of 1500 km² pertaining to the city of Delhi, India. Delhi is a mega-city of 16 million inhabitants in constant, rapid expansion (Census Organization of India 2011). The overall city comprises both urban and semi-urban areas under poor solid waste management, which affords plenty of food to Black Kites in the form of rubbish, carrion and remains from slaughterhouses. The climate is semi-arid, with 64 cm of annual precipitation, mainly concentrated in July and August. Temperature ranges from a mean maximum of 39.6°C to a minimum of less than 8.2°C in the winter (India Meteorological Department 2013). The vegetation of the general region falls within the 'northern tropical thorn forest' category (Champion & Seth 1968).

Field procedures

Because many areas of the city were private properties not accessible to the public, it was impossible to design a very large continuous study area. Also, because Black Kites in our area can attain extremely high densities, small-sized plots distributed over a wide area were judged to be better suited to sample all available conditions than a single continuous plot of necessarily limited extent. Therefore, we designed a network of 24 sample plots, each one of approximately 1 km² of homogenous accessibility and distributed throughout the city covering all types of potential nesting habitats. However, a standardized shape or a standardized

surface of 1 km² could not be attained for all plots because of constraints imposed by private properties and logistical difficulties of access. Private properties had similar landscape features to the surrounding areas of the city and we are confident that their exclusion did not bias our density estimates. However, because of the above, nests which were located at the periphery of each sample plot were not employed to generate estimates of nest spacing (nearest neighbour distance henceforth referred as NND), unless a complete nest census had been conducted also for the area bordering the quadrat.

We surveyed each quadrat repeatedly every few weeks, starting from the pre-incubation period, by walking slowly and carefully inspecting all potential nest structures (trees, buildings, towers, etc.). Structures were classified as active nests when a kite individual or pair was repeatedly observed to perch in the nest or its immediate surroundings, or to add material to the nest. Once found, nests were checked by climbing to them, observing them from nearby vantage points, or through an eight-meter telescopic rod equipped with a video-recording camera. Nests were checked approximately every eight days. However, because of time, safety, accessibility and manpower limitations, data on breeding success were collected only at a sub-sample of nests.

A nest was classified as depredated when we found remains of plucked chicks. Cases of brood reduction (death of one chick, often caused by its siblings, subsequently fed to other nestlings) were not classified as predation events. Hatching date was calculated by backdating from the feather development of nestlings first observed when <15 day old and by comparison to reference information in Desai & Malhotra (1977), Cramp & Simmons (1980), Hiraldo *et al.* (1990) and personal data by one of the authors (F.S.). Laying date was estimated by subtracting 30 day, the average incubation period (Viñuela 1997), from hatching date. During each visit, we collected prey remains found inside and under nests and identified them to the genus or species level assuming the smallest possible number of individuals. These items were used to estimate each prey percentage contribution by number or by mass to the diet of Black Kites.

Terminology follows Steenhof (1987): a territorial pair was one that built a nest and then did or did not lay a clutch; a breeding or reproductive pair was one which laid eggs; a successful pair was one which raised at least one nestling until it was 40 day old; and breeding success was the percentage of successful

territorial pairs. There was no need to correct the estimates of breeding success through Mayfield estimators, because all plots were surveyed repeatedly from the pre-laying period onwards, and because nests were easy to find and were checked very frequently (approximately every eight days). Density was calculated as number of territorial pairs per unit area and expressed as number of pairs/km². The difference in breeding success between nests located in trees and nests built on artificial structures was tested by means of a Z-test (Zar 1984). Throughout, means are given ± 1 se, tests are two-tailed, and statistical significance was set at $\alpha \leq 0.05$.

RESULTS

Cumulatively, we censused 244 Black Kite nests in 2013. Out of these, 223 (91.4%) were located on trees and the rest on artificial structures (17 on electricity pylons and 4 on telephone metal towers). Out of 223 tree nests, 35.5% were built on *Eucalyptus* spp., 23% on *Ficus* spp., 13.8% on Neem (*Azadiracta indica*), 12.7% on Jamun (*Syzygium cumini*) and 8.3% on Keekar (*Prosopis juliflora*). The mean nest density was 15.1 ± 7.9 pairs/km² and varied between 0 and 67.1 nests/km² ($n = 24$ plots). Mean NND for the whole population was 133 ± 15 m and ranged between 5 and 2315 m ($n = 207$ pairs).

A subset of 151 nests was closely monitored for breeding success. The overall mean laying date was 31 January ($n = 65$, se = 3.3 days; range 19 December–13 April) and the laying season lasted almost 4 months (115 days), with a pronounced peak between the second half of January and first half of February (Fig. 1). When mean monthly temperature and rainfall were super-imposed on the laying frequency (Fig. 2), kites seemed to concentrate clutch initiation before the temperatures became excessively high and before the start of the Monsoon rains in June–July. The percentage of clutches initiated each month was negatively related to the minimum monthly temperature (linear regression: $B = -1.37 \pm 0.35$; B for constant = 34.21 ± 7.14 ; $n = 12$; Bonferroni-corrected $P = 0.006$; $R^2 = 0.56$) and quadratically related to the maximum monthly temperature (quadratic regression: B for linear term = -11.86 ± 3.66 ; Bonferroni-corrected $P = 0.02$; B for quadratic term = 0.17 ± 0.06 ; Bonferroni-corrected $P = 0.02$; B for constant = 211.37 ± 54.04 ; $n = 12$; $R^2 = 0.77$), while egg laying stopped with the commencement of the rains and was initiated again only after the monsoon season. Finally, the

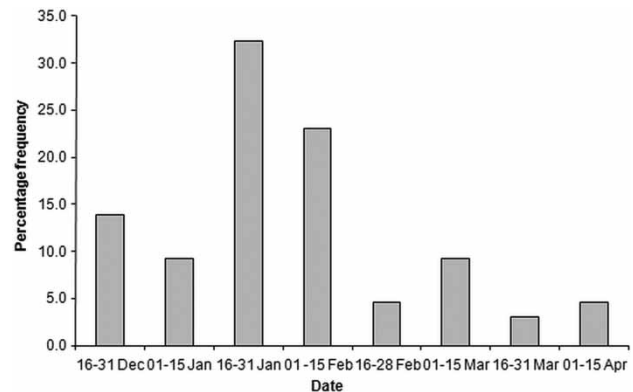


Figure 1. Temporal frequency of laying dates in the Black Kite population of Delhi (India) in 2013 ($n = 65$).

number of young fledged by each pair declined with laying date (linear regression: $B = -0.13 \pm 0.03$; B for constant = 1.66 ± 1.77 ; $n = 65$, $P = 0.001$; $R^2 = 0.17$).

Mean clutch size was 2.09 ± 0.06 ($n = 100$). Mean hatching success was $64.6 \pm 4.65\%$ ($n = 72$ nests). Of 137 chicks first observed when less than five days old, three were depredated (all from a single nest) and six were subsequently observed dead in the nest or simply disappeared, probably because of sibling aggression (Viñuela 2000). The mean percentage of nestlings lost by brood reduction was 0.16 ± 0.04 per brood ($n = 91$ nests). The mean number of fledged young was 0.73 ± 0.07 per territorial pair ($n = 151$), 1.09 ± 0.06 per breeding pair ($n = 100$) and 1.53 ± 0.04 per successful pair ($n = 72$). Forty-eight per cent of territorial pairs successfully raised their nestlings to fledging age ($n = 151$). There was a trend for breeding success to be higher for nests on trees than for nest on the artificial structures (46% vs. 27.8%; $Z = 1.8$, $P = 0.07$, n for tree nests = 130, n for artificial substrate = 21).

Black Kite diet included all vertebrate classes but was strongly dominated, both by mass and number, by three main items: (1) remains from slaughterhouses, mainly in the form of compact chunks of meat; (2) rats and (3) medium-sized urban birds, such as doves and pigeons (Table 1).

DISCUSSION

Our study confirmed that Black Kites maintained extremely high breeding densities throughout the city of Delhi, as already observed in the 1970s (Galushin 1971). When compared with data from other populations (reviewed in Table 2), the density observed in the urban environment of Delhi was

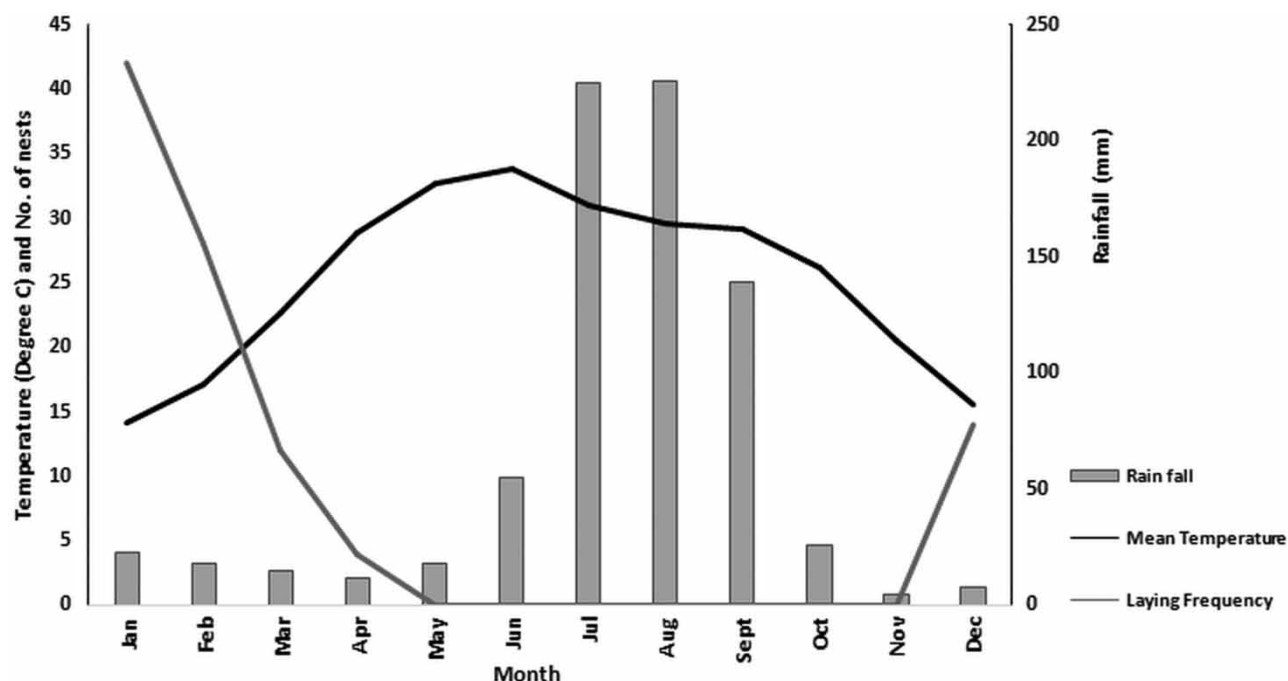


Figure 2. Mean temperature, monthly rainfall and Black Kite laying frequency in Delhi (weather data from India Meteorological Department 2013).

Table 1. Diet of breeding Black Kites in Delhi, India (2012–2013), as estimated by food remains collected inside and under the nest.

Prey category	Frequency by number (%)	Frequency by mass (%)
Fish ^a	0.8	1.0
Amphibians ^b	0.7	0.7
Reptiles ^c	0.7	0.3
Birds	24.6	31.9
(i) Rock Pigeon (<i>Columba livia</i>)	13.1	16.2
(ii) Collared Dove (<i>Streptopelia decaocto</i>)	4.1	3.3
(iii) Other birds ^d	7.4	12.4
Mammals ^e	9.8	20.2
Scavenged meat ^f	63.4	45.9
(i) Meat scraps	47.1	35.6
(ii) Domestic chicken	11.5	6.1
(iii) Cattle ^g	4.1	3.5
(iv) Fish ^h	0.7	0.7

^aUnidentified fish ($n = 1$).

^bIndian bull-frog ($n = 1$).

^cCommon house gecko ($n = 1$).

^dMoorhen (*Gallinula chloropus*) ($n = 1$), Indian Roller (*Coracias benghalensis*) ($n = 1$), Unidentified birds ($n = 7$).

^eMammals which were unlikely to be consumed as carrion. Includes: Norway rat (*Rattus norvegicus*) ($n = 11$) and Palm squirrel (*Funambulus pennantii*) ($n = 1$).

^fPrey items that were considered to have been collected as carrion from local rubbish dumps and slaughterhouses.

^gBuffalo ($n = 2$), Goat ($n = 3$).

^hLarge unidentified fish skin, likely from fish market.

higher than any previously published estimate. This is then, probably, the highest density ever recorded over a large, continuous area for any bird of prey of this size. The capability to attain such a high population-level over such a large region is likely to be promoted by a combination of at least three factors. (1) First, the rubbish management plans of such a rapidly developing mega-city are inevitably poor, which results in a network of enormous, legally authorized rubbish dumps coupled with hundreds of smaller, and often illegal sites where garbage is dumped daily. At an even finer-scale, private individuals, families and shops often leave their daily garbage directly in the streets, resulting in a network of ephemeral, small piles of food. In turn, these must promote large populations of potential prey species, such as rats and pigeons. All the above, coupled with the high abundance of meat and fish shops throughout the city, sets an ideal scenario of enormous food availability for an opportunistic predator and facultative scavenger. (2) Second, the attitudes of local people towards kites, and wildlife in general, are extremely positive and tolerant, even despite the fact that some kites can be very aggressive in defending their nest against nearby passers-by. We are not aware of any cases of persecution of kites in Delhi, which is confirmed by the relative absence of

Table 2. Breeding density and nest spacing of Black Kite populations in Europe and India (Delhi), 1966–2013.

Area (period)	Habitat	Density (pr/10 km ²) (n)	NDD in meters (n)
Delhi, India (2013) ¹⁷	U	150 (244)	133 (207)
Delhi, India (1967–1969) ³	U	161 (~560)	–
NZP, India (1979) ¹⁶	U	250 (18–21)	–
NZP, India (2013) ¹⁷	U	264 (70)	–
Matas Gordas, Spain (1987–1989) ¹⁰	M	70–150 (21– 45)	–
Matas Gordas, Spain (1992–2000) ¹⁵	M	100.8 (515)	–
Doñana, Spain (1981–1984) ⁸	M	26.7 (80)	206 (47) ^a
RBD, Spain (1989–2000) ¹⁵	M	15.1 (1059)	–
Lac Lemán, Switzerland (1975– 1990) ¹¹	F	10.1 (319)	–
Neuchâtel, Switzerland (1968) ⁵	FL	7.1 (337)	–
Lorraine, France (1966) ¹	WP	4.5 (66)	–
Rhône Plain, France (1970) ⁵	RP	60.9 (140)	–
Limousin, France (1976–1978) ⁴	PW	1.0 (21)	–
Lake Lugano, Italy (1992–1996) ¹³	WL	2.4–3.8 (27– 41)	441 (175)
Lake Lugano, Italy (1992–2003) ¹⁵	WL	2.9 (365)	–
Lake Maggiore, Italy (1996–2000) ¹⁴	WL	–(24)	–
Lake Como, Italy (1996–2000) ¹⁴	WL	4.7 (40)	–
Lake Iseo, Italy (1996–2000) ¹⁴	WL	3.5 (48)	–
Lake Idro, Italy (1997–2001) ¹⁴	WL	6.7 (37)	–
Lake Garda, Italy (1997–2000) ¹⁴	WL	1.5 (18)	–
Sarca Valley, Italy (1997–2003) ¹⁴	WL	1.3 (88)	–
Castelporziano, Italy (1991–1992) ⁹	WF	3.3 (16)	103 (16) ^b
Monti della Tofa, Italy (1973–1980) ⁷	WP	0.5 (42)	–
Constance Lake, Germany (1968– 1969) ²	FL	1.9–2.2 (25– 30)	–
Drömling, Germany (1993–1994) ¹²	F	0.7 (8)	2330 (8) ^c
Brandenburg, Germany (1979) ⁶	F	0.7 (215)	–

Notes: Density was expressed as territorial pairs/10 km² for clarity of presentation. The 2013 data from the current study are presented twice in the table: (i) for the whole study area, i.e. representative of the whole Delhi population; and (b) for the high-density sector of the New Delhi National Zoological Park (NZP), in order to make them comparable to historical data from the 1970s by Malhotra (2007). Habitats are U, Urban; M, Marshland; FL, Farmland and Lake; WL, Woodland and Lake; F, Farmland; WP, Woodland and Pasture; WF, Woodland and Farmland; FL, Farmland and Lake; PW, Pasture and Woodland; RP, River Plain.

^aEstimate from Bustamante & Hiraldo (1990), for the period 1985–1988.

^bA single colony.

^cCalculated from the published map.

¹Thiollay (1967), ²Heckenroth (1970), ³Galushin (1971), ⁴Nore (1979), ⁵Sermet (1980), ⁶Fiuczynski (1981), ⁷Petretti & Petretti (1981),

⁸Hiraldo et al. (1990), ⁹De Giacomo et al. (1993), ¹⁰Viñuela et al. (1994), ¹¹Henrioux & Henrioux (1995), ¹²Seelig et al. (1996),

¹³Sergio & Boto (1999), ¹⁴Sergio et al. (2003), ¹⁵Sergio et al. (2005), ¹⁶Malhotra (2007), ¹⁷This study.

fear of humans by most kites in comparison to European conspecifics. (3) Third, the city provides an environment with a low abundance of potential predators. The only potential nest predators known to occur locally are Indian Eagle Owls *Bubo bubo*

bengalensis, House Crows *Corvus splendens* and Rhesus Macaques *Macaca mulatta*. The latter two species can be locally abundant, but are often deterred by the very aggressive and effective nest defence behaviour of parent kites.

When compared to historical records, the high density we recorded seemed remarkably stable over several decades. Rapid city-wide surveys and data from the New Delhi Zoological Park suggested only slightly higher densities in the 1970s than currently observed (Galushin 1971, Desai & Malhotra 1979; see Table 2). This is despite enormous changes in the city's dimensions, population size and management, and despite the recent, virtual extinction of the locally abundant populations of a potential trophic competitor, the White-rumped Vulture *Gyps bengalensis*, the former primary scavenger (Prakash et al. 2003, Naoraji 2006). The kite population thus seems very resilient to change in terms of overall density.

The laying season was protracted over almost four months, probably as a result of the long period of warm, favourable climate and of the stable food supply provided by the urban environment (Fig. 1). The temporal peak and range of laying dates seemed to be arranged so that most nestlings fledged well before the high temperatures and the marked peak in precipitation caused by Monsoon rains in July–August (Fig. 2). The negative effect of high temperatures and rainfall on kite foraging performance, egg viability and breeding success has been reported for various European populations (Hiraldo et al. 1990, Viñuela 2000, Sergio 2003). The observed, lengthy range of laying dates compares to a duration of the laying season of 28 days for kite populations of the Italian Alps and to 2.8 months for the population of Doñana National Park, in the extreme south of Europe (F. Sergio, pers. data). This suggests a North-South latitudinal gradient in the length of kites' breeding seasons. Protracted breeding seasons are increasingly reported as progressively more studies of birds of prey are conducted in tropical or more southern latitudes (Simmons 2000, Ogada & Kibuthu 2012).

When compared to other populations (review in Table 3), our estimates of breeding success were lower than in other studies and this may be a consequence of density-dependent processes in a crowded, saturated population (Newton 1998). The fact that similarly low levels of reproduction were reported for another saturated population (Doñana, Sergio et al. 2011) lends support to this impression. However, in the absence of more information, other alternative explanations

Table 3. Productivity of Black Kite populations in Europe and Asia, 1966–2013.

Area (period)	Habitat (n)	Clutch size	Hatching success ^a (eggs)	Breeding success (%)	Mean number of fledged young		
					Territorial pair	Breeding pair	Successful pair
Delhi, India (2013) ¹¹	U (151)	2.09 (100) ^b	68% (157) ^b	48	0.73	1.09 (100) ^b	1.52 (72) ^b
NZP, India (1973–1976) ²	U (45)	2.3 (60) ^b	55% (102) ^b	–	0.98	–	–
NZP, India (2013) ¹¹	U(46)	2.04 (36)	62% (55) ^b	59	0.78	0.95 (38) ^b	1.44 (25) ^b
RBD, Spain (1989–2000) ¹⁰	WL(1059)	2.02	67.4 (416)	41	0.59	0.71	1.43
Matas Gordas, Spain (1992–2000) ¹⁰	GM(515)	2.12	70.3 (232)	44	0.61	0.85	1.46
Germany (1992–1995) ^{7c}	– (599)	–	–	79	1.63	–	2.07 (471) ^b
Limousin, France (1976–1978) ³	PW (22)	–	–	68	–	1.32	1.93 (15) ^b
Berlin, Germany (1940–1979) ⁴	F (215)	–	–	62	1.20	–	1.90 (133) ^b
Lake Lugano, Italy (1992–1996) ⁹	WL (143)	2.29 (42) ^b	84% (96) ^b	55	0.97	1.1 (95) ^b	1.78 (78) ^b
Lake Lugano, Italy (1992–2003) ¹⁰	WL (315)	2.3	74 (88)	50	0.90	1.24	1.80
Lake Maggiore, Italy (1996–2000) ¹⁰	WL (30)	–	–	50	0.87	–	1.73
Lake Como, Italy (1996–2000) ¹⁰	WL (40)	–	–	48	0.75	–	1.58
Lake Iseo, Italy (1996–2000) ¹⁰	WL (48)	–	–	38	0.48	–	1.10
Lake Idro, Italy (1997–2001) ¹⁰	WL (37)	–	–	59	1.05	–	1.63
Lake Garda, Italy (1997–2000) ¹⁰	WL (18)	–	–	44	0.83	–	2.14
Sarca Valley, Italy (1997–2003) ¹⁰	WL (88)	–	–	40	0.63	–	1.62
Slovakia (1975–1989) ⁵	– (162)	2.98 (44) ^b	–	–	–	2.31	–
Lac Lemman, Switzerland (1975–1990) ⁸	FL (165)	2.25	–	–	–	2.02	–
Lorraine, France (1966) ¹	WP (66)	2.26 (45) ^b	–	–	1.32	1.58 (55) ^b	–
Nagasaki, Japan (1983–1986) ⁶	FP (32)	2.18 (28) ^b	79% (61) ^b	75	1.00	1.14 (28) ^b	1.33 (24) ^b

Notes: The 2013 data from the current study are presented twice in the table: (i) for the whole study area, i.e. representative of the whole Delhi population; and (ii) for the high-density sector of the New Delhi National Zoological Park (NZP), in order to make them comparable to historical data from the 1970s by Desai & Malhotra (1979). Habitats are U, Urban; GM, Grassland and Marshland; FL, Farmland and Lake; WL, Woodland and Lake; F, Farmland; WP, Woodland and Pasture; FL, Farmland and Lake; PW, Pasture and Woodland; FP, Fishing Port.

^aData on hatching success not shown in the table: 75% ($n = 36$ eggs from 14 nests, Hakel, Germany, 1957; Stubbe 1961) and 64% ($n = 28$ eggs from 10 nests, Lazio, Italy, date unknown; Petretti 1992).

^bSample size (when different from that in column 'Habitat (n)').

^cData also from Mammen & Stubbe (1995, 1996).

¹Thiollay (1967), ²Desai & Malhotra (1979), ³Nore (1979), ⁴Fiuczynski (1981), ⁵Danko (1989), ⁶Koga et al. (1989), ⁷Gedeon (1994)^c, ⁸Henrioux & Henrioux (1995), ⁹Sergio & Boto (1999),

¹⁰Sergio et al. (2005), ¹¹This study.

cannot be discounted: for example, it is not known whether a diet based in large portion on rubbish and meat produced for human consumption could spread pathogens or toxic substances among the offspring.

Finally, the observed diet composition confirmed the full dependence of the local kite population on urban resources, such as meat scraps from slaughterhouses or prey species which were extremely abundant within the city, such as rats, pigeons and doves. The current picture of the diet does not suggest that kites range frequently, if at all, out of the city to capture wild prey in surrounding rural areas. This confirms that the high density attained within the urban setting is likely promoted by attraction to a dense food source.

In summary, extensive foraging opportunities, a stable favourable climate, absence of human persecution and low density of potential predators have probably contributed to one of the densest raptor populations of the world. The current conservation status of the studied population seems satisfactory, but recent urban development is causing extreme and almost complete removal of mature trees in some sectors of the city. In turn, this could limit the kite population in the future, or trigger local declines and re-distributions, especially when considering that artificial structures do not seem to fully compensate for tree absence (authors' pers. data). Thus, given the abundance of the species and the current urban sanitary levels, the ecological service provided by kites through removal of organic rubbish must be valuable, suggesting the need for ecologically sensitive urban planning of the remaining green areas. This calls for the importance of continued monitoring of the population and its nesting requirements in future years.

ACKNOWLEDGEMENTS

We thank W. Cresswell and three anonymous reviewers for improving the manuscript with their comments. We thank the Forest Departments of the Government of NCT, Delhi and Uttar Pradesh; Shri. Amitabh Agnihotri (Director of the National Zoological Park, New Delhi); the Administrative Officer of Miranada House: University of Delhi (DU); various other landowners, managers and government officials for permissions and logistic support. We heartedly thank for help in the field our field assistant Vishnu Narayan, Dr A. Tanferna and the following volunteers of the 'Black Kite Project Group' from Sri Venkateswara College (DU) and the University of Delhi: M. Singh, N. Goyal, S. Gupta, E. Bhartia, A. Yadav, C. Prajapati, D. Pal, V. Sindhi, K. Wadhwa, D. Ramanan, S. Prajapati, N. Verma, J. Sungra, B. Roy, A. Bedi,

A. Mandal, V. Gupta, A. Dutta, P. Kumar, Raju, D. Thakur, G. Singh, Saubhagya, G. Vashishtha and M. Garg.

FUNDING

The study was funded by the Wildlife Institute of India and Raptor Research and Conservation Foundation (RRCF, Mumbai). Funding for travelling and fieldwork by F. Sergio was afforded by Project RNM-7307 of the Junta de Adalucia and CGL2011-28103 of the Spanish Ministry of Science and Innovation.

REFERENCES

- Abdulali, H.** 1968. Extension of the range of the large Indian Kite *Milvus migrans lineatus* (Gray). *J. Bombay Nat. History Soc.* **65**: 774.
- Abdulali, H.** 1972. Some bird notes by W.F. Sinclair. *J. Bombay Nat. History Soc.* **69**: 422–424.
- Ali, S.** 1926. Mating habits of the Common Kite *Milvus migrans govinda*. *J. Bombay Nat. History Soc.* **31**: 524–526.
- Ali, S. & Ripley, S. D.** 1983. *Handbook of the Birds of India and Pakistan: together with those of Bangladesh, Nepal, Sikkim and Sri Lanka* (Vol. 1: Divers and Hawks). Compact ed. Delhi (IN): Oxford University Press. p. 226–229.
- Bijlsma, R.G.** 1997. Black Kite. In Hagemeyer, W.J.M. & Blair, M.J. (eds.) *The EBCC Atlas of European Breeding Birds, their Distribution and Abundance*, 132–133. T & AD Poyser, London.
- Blanco, G.** 1997. Role of refuse as food for migrant, floater and breeding Black Kites (*Milvus migrans*). *J. Raptor Res.* **31**: 71–76.
- Brown, L.H., Urban, E.K. & Newman, K.** 1982. *The Birds of Africa*, Vol. 1. Academic Press, London.
- Bustamante, J. & Hiraldo, F.** 1990. Adoptions of fledglings by Black and Red Kites. *Anim. Behav.* **39**: 804–806.
- Census Organization of India.** 2011. Census of India. Available from: <http://censusindia.gov.in/2011census> [accessed 27 September 2013].
- Champion, H.G. & Seth, S.K.** 1968. *A Revised Survey of the Forest Types of India*. Manager of Publications, Government of India, New Delhi.
- Cramp, S. & Simmons, K.E.L.** 1980. *Handbook of the Birds of Europe, the Middle East and North Africa*, Vol. 2. Hawks and Bustards. Oxford University Press, Oxford.
- Danko, Š.** 1989. Five young in the nest of a Black Kite (*Milvus migrans*). *Buteo* **4**: 87–92.
- De Giacomo, U., Martucci, O. & Tinelli, A.** 1993. L'alimentazione del Nibbio bruno (*Milvus migrans*) nella Tenuta di Castelporziano (Roma). *Avocetta*. **17**: 73–78.
- Desai, J.H. & Malhotra, A.K.** 1977. Growth and development of the Pariah Kite *Milvus migrans govinda*. *Miscellaneous Rep. Yamashina Inst. Ornithol.* **9**: 217–226.
- Desai, J.H. & Malhotra, A.K.** 1979. Breeding biology of the Pariah Kite *Milvus migrans* at Delhi Zoological Park. *Ibis* **121**: 320–325.
- Ferguson-Lees, J. & Christie, D.A.** 2001. *Raptors of the World*. Houghton Mifflin Company, New York.
- Fischer, C.E.C.** 1906. Flocking of Kites. *J. Bombay Nat. History Soc.* **17**: 525–526.
- Fiuczynski, V.** 1981. Berliner milan-chronik (*Milvus migrans* and *Milvus milvus*). *Beitr. Vogelkd* **27**: 161–196.
- Galushin, V.M.** 1971. A huge urban population of birds of prey in Delhi India. *Ibis* **113**: 522.
- Gedeon, K.** 1994. Monitoring Greifvögel und Eulen. Grundlagen und Möglichkeiten einer Langfristigen Überwachung von Bestandsgrößen

- und Reproduktionsdaten Jahresber. *Monitoring Greifvögel Eulen Europas* **1**: 1–118.
- Hanxwell, T.A.** 1892. Nest and eggs of the crested Black Kite. *J. Bombay Nat. History Soc.* **07**: 403–404.
- Heckenroth, V.** 1970. Der Greifvögelbestand des Bodanrücks (Bodensee) 1968 and 1969. *Anz. Ornithol. Ges Bayern* **9**: 47–51.
- Henrioux, P. & Henrioux, J.** 1995. Seize ans d'étude sur les rapaces diurnes et nocturnes dans l'Ouest lemanique (1975–1990). *Nos Oiseaux* **43**: 1–26.
- Hiraldo, F., Veiga, J.P. & Manez, M.** 1990. Growth of nestling Black Kites *Milvus migrans*: effects of hatching order, weather and season. *J. Zool. Lond.* **222**: 197–214.
- India Meteorological Department.** 2013. <http://amssdelhi.gov.in/climatology/sfd1.htm> [accessed 27 September 2013].
- Koga, K., Siraishi, S. & Uchida, T.A.** 1989. Breeding ecology of the Black-eared Kite *Milvus migrans lineatus* in the Nagasaki Peninsula, Kyushu. *Jpn. J. Ornithol.* **57**: 57–66.
- Mahabal, A. & Bastawade, D.B.** 1985. Population ecology and communal roosting behaviour of Pariah Kite *Milvus migrans govinda* in Pune (Maharashtra). *J. Bombay Nat. History Soc.* **82**: 337–346.
- Malhotra, A.K.** 1991. Site fidelity and power of recognition in Pariah Kite *Milvus migrans govinda*. *J. Bombay Nat. History Soc.* **87**: 458.
- Malhotra, A.K.** 2007. Tiger of sky-Pariah Kite. PhD Thesis, Shilalekh Publishers, Delhi.
- Mammen, U. & Stubbe, V.** 1995. Jahresbericht 1994 zum monitoring Greifvögeln und Eulen Europas Jahresber. *Monitoring Greifvögel Eulen Europas* **7**: 1–78.
- Mammen, U. & Stubbe, V.** 1996. Jahresbericht 1995 zum monitoring Greifvögeln und Eulen Europas Jahresber. *Monitoring Greifvögel Eulen Europas* **8**: 1–92.
- Naorji, R.** 2006. *Birds of Prey of the Indian Subcontinent*. Christopher Helm/A&C Black Publishers Ltd., London.
- Newton, I.** 1998. *Population Limitation in Birds*. Academic Press, London.
- Nore, T.** 1979. Rapaces diurnes communs en Limousin pendant la periode de nidification (Buse, Bondre, Milan noir, Busards saint-martin et Cendres). *Alauda* **47**: 183–194.
- Ogada, D.L. & Kibuthu, P.M.** 2012. Breeding ecology of Mackinder's Eagle-Owls (*Bubo capensis mackinderi*) in farmlands of central Kenya. *J. Raptor Res.* **46**: 327–335.
- Ortlieb, R.** 1998. *Der Schwarzmilan*. Die Neue Brehm-Bücherei, Hohenwarsleben, Germany.
- Owino, A., Biwott, N. & Amutete, G.** 2004. Bird strike incidents involving Kenya Airways flights at three Kenyan airports, 1991–2001. *African J. Ecol.* **42**: 122–128.
- Petretti, F.** 1992. Nibbio bruno. In Brichetti, P., De Franceschi, P. & Baccetti, N. (eds.) *Fauna d'Italia*, 459–465. Edizioni Calderini, Bologna, Italy.
- Petretti, A. & Petretti, F.** 1981. A population of diurnal raptors in central Italy. *Gerfaut* **71**: 143–156.
- Prakash, V., Pain, D.J., Cunningham, A.A., Donald, P.F., Prakash, N., Verma, A., Gargia, R., Sivakumar, S. & Rahmani, A.R.** 2003. Catastrophic collapse of Indian White Backed (*Gyps bengalensis*) and Long Billed (*Gyps indicus*) vulture population. *Biol. Conserv.* **109**: 381–390.
- Satheesan, S.M.** 1996. Raptors associated with airports and aircraft. In D. M. Bird, D. E. Varland, and J. J. Negro (eds.) *Raptors in human landscapes: adaptations to built and cultivated environments: Adaptations to built and cultivated environments*, 315–323. Academic Press, London.
- Seelig, K., Benecke, H., Braumann, F. & Nicolm, B.** 1996. *Die Vogel im Naturpark Drömling*. Abh. Ber. Mus. Heineanum 3, Sonderh, Germany.
- Sergio, F.** 2003. From individual behaviour to population pattern: weather-dependent foraging and breeding performance in Black Kites. *Animal Behav.* **66**: 1109–1117.
- Sergio, F. & Boto, A.** 1999. Nest dispersion, diet and breeding success of Black Kites (*Milvus migrans*) in Italian Pre-Alps. *J. Raptor Res.* **33**: 207–217.
- Sergio, F., Pedrini, P. & Marchesi, L.** 2003. Reconciling the dichotomy between single species and ecosystem conservation: Black Kites and eutrophication in pre-Alpine lakes. *Biol. Conserv.* **110**: 101–111.
- Sergio, F., Blas, J., Forero, M., Fernández, N., Donazar, J.A. & Hiraldo, F.** 2005. Preservation of wide-ranging top predators by site-protection: Black and Red kites in Doñana national park. *Biol. Conserv.* **125**: 11–21.
- Sergio, F., Blas, J., López, L., Tanferna, A., Díaz-Delgado, R., Donazar, J.A. & Hiraldo, F.** 2011. Coping with uncertainty: breeding adjustments to an unpredictable environment in an opportunistic raptor. *Oecologia* **166**: 79–90.
- Sermet, E.** 1980. Milan noir. In Schifferli, A., Göröudet, P. & Winkler, R. (eds.) *Arias des oiseaux nicheurs de Suisse*, 88–89. Station Ornithologique de Sem-pach, Sempach, Switzerland.
- Simmons, R.E.** 2000. *Harriers of the World: Their Behaviour and Ecology*. Oxford University Press, London, United Kingdom.
- Steenhof, K.** 1987. Assessing raptor reproductive success and productivity. In B.A. Giron, P., Millsap B. A., Kline, K.W. & Bird D.M. (eds.) *Raptor Management Techniques Manual*, 157–170. Natl. Wildl. Fed., Washington, DC.
- Stubbe, V.** 1961. Die Besiedelungsdichte eines Abgeschlossenen Waldgebietes (Hakel) mit Greifvögeln im Jahre 1957. *Beitr. Vogelkd* **7**: 155–224.
- Thiollay, J.-M.** 1967. Ecologie d'une population de rapaces diurnes en Lorraine. *La Terre et la Vie*. **114**: 116–183.
- Thiollay, J.-M. & Bretagnolle, V.** 2004. *Rapaches nicheurs de France: distribution, effectifs et conservation*. Delachaux et Niestlé, Paris, France.
- Viñuela, J.** 1997. Laying order affects incubation duration in the Black Kite (*Milvus migrans*): counteracting hatching asynchrony? *Auk* **114**: 192–199.
- Viñuela, J.** 2000. Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. *Behav. Ecol. Sociobiol.* **45**: 333–343.
- Viñuela, J., Villafuerte, R. & De Le Court, C.** 1994. Nesting dispersion of a Black Kite population in relation to location of rabbit warrens. *Can. J. Zool.* **72**: 1680–1683.
- Zar, J.H.** 1984. *Bio-Statistical Analysis*, 283. Prentice-Hall, Englewood Cliffs, NJ.

(MS received 18 October 2013; revised MS accepted 15 December 2013)

Chapter 2

Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools

Nishant Kumar, Urvi Gupta, Yadvendradev Jhala, Qamar Qureshi, Andrew Gosler & Fabrizio Sergio

*Originally published on December 18, 2017; Volume 51(2), **Urban Ecosystems**.*



Abstract

Research in urban ecology is growing rapidly in response to the exponential growth of the urban environment. However, few studies have focused on tropical megacities, and on the interplay between predators' habitat selection and human socio-economic aspects, which may mediate their resilience and coexistence with humans. We examined mechanisms of breeding habitat selection by a synanthropic raptor, the Black Kite *Milvus migrans*, in Delhi (India) where they mainly subsist on: (1) human refuse and its associated prey-fauna, and (2) ritualised feeding of kites, particularly practiced by *Muslims*. We used mixed effects models to test the effect of urban habitat configuration and human practices on habitat selection, site occupancy and breeding success. Kite habitat decisions, territory occupancy and breeding success were tightly enmeshed with human activities: kites preferred areas with high human density, poor waste management and a road configuration that facilitated better access to resources provided by humans, in particular to Muslim colonies that provided ritual subsidies. Furthermore, kites bred at 'clean' sites with less human refuse only when close to Muslim colonies, suggesting that the proximity to ritual-feeding sites modulated the suitability of other habitats. Rather than a nuisance to avoid, as previously portrayed, humans were a keenly-targeted foraging resource, which tied a predator's distribution to human activities, politics, history, socio-economics and urban planning at multiple spatio-temporal scales. Many synurbic species may exploit humans in more subtle and direct ways than was previously assumed, but uncovering them will require greater integration of human socio-cultural estimates in urban ecological research.

Keywords: Urban ecology; Food subsidies; Muslim; Ritual feeding; Synurbic; Urbanization



A view from a Black Kite nest on a pylon in Delhi, depicting the selection pressures offered by steep habitat edges (Chapter 2 and 5).



Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools

Nishant Kumar^{1,2} · Urvi Gupta^{2,3} · Yadvendradev V. Jhala² · Qamar Qureshi² · Andrew G. Gosler^{1,4} · Fabrizio Sergio⁵

Published online: 18 December 2017
© The Author(s) 2017. This article is an open access publication

Abstract

Research in urban ecology is growing rapidly in response to the exponential growth of the urban environment. However, few studies have focused on tropical megacities, and on the interplay between predators' habitat selection and human socio-economic aspects, which may mediate their resilience and coexistence with humans. We examined mechanisms of breeding habitat selection by a synanthropic raptor, the Black Kite *Milvus migrans*, in Delhi (India) where kites mainly subsist on: (1) human refuse and its associated prey-fauna, and (2) ritualised feeding of kites, particularly practised by *Muslims*. We used mixed effects models to test the effect of urban habitat configuration and human practices on habitat selection, site occupancy and breeding success. Kite habitat decisions, territory occupancy and breeding success were tightly enmeshed with human activities: kites preferred areas with high human density, poor waste management and a road configuration that facilitated better access to resources provided by humans, in particular to Muslim colonies that provided ritual subsidies. Furthermore, kites bred at 'clean' sites with less human refuse only when close to Muslim colonies, suggesting that the proximity to ritual-feeding sites modulated the suitability of other habitats. Rather than a nuisance to avoid, as previously portrayed, humans were a keenly-targeted foraging resource, which tied a predator's distribution to human activities, politics, history, socio-economics and urban planning at multiple spatio-temporal scales. Many synurbic species may exploit humans in more subtle and direct ways than was previously assumed, but uncovering them will require greater integration of human socio-cultural estimates in urban ecological research.

Keywords Urban ecology · Food subsidies · Muslim · Ritual feeding · Synurbic · Urbanization

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s11252-017-0716-8>) contains supplementary material, which is available to authorized users.

✉ Nishant Kumar
nishant.kumar@zoo.ox.ac.uk

Urvi Gupta
urvi.gupta@ouce.ox.ac.uk

Yadvendradev V. Jhala
jhalay@wii.gov.in

Qamar Qureshi
qnq@wii.gov.in

Andrew G. Gosler
andrew.gosler@zoo.ox.ac.uk

Fabrizio Sergio
fsergio@ebd.csic.es

¹ Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

² Wildlife Institute of India, Post Box # 18, Chandrabani, Dehradun, Uttarakhand PIN-248001, India

³ School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK

⁴ School of Anthropology and Museum Ethnography, Institute of Human Sciences, 58a Banbury Rd, Oxford OX2 6QS, UK

⁵ Department of Conservation Biology, Estacion Biologica de Doñana-CSIC, C/ Americo Vespucio, s/n, 41092 Sevilla, Spain

Introduction

Urban ecosystems are spreading rapidly, with more than 50% of the global human population currently concentrated in cities, a figure estimated to reach 66% by 2050 (United Nations 2014). Ninety-eight percent of this net increase is expected to happen in cities in developing countries (Grimm et al. 2008), so that by the middle of the twenty-first century 75% of urban dwellers will be located in Asia and Africa (Anonymous 2016). Such urban sprawl has well-demonstrated ecological consequences, including disruption of energy flow and nutrient cycles, habitat degradation, increased carbon emissions, and the extinction of many species (e.g. Pickett et al. 2001; McKinney 2010). Nevertheless, some animal species have managed to adapt and thrive under such conditions (Lepczyk et al. 2017), some for example can take advantage of human waste and reach densities that are not otherwise encountered (Brook et al. 2003; Gangoso et al. 2013; Inger et al. 2016). These urban exploiters are often alien invaders seen as ‘nuisances to eradicate’ (e.g. Belant 1997; Brook et al. 2003; Kurosawa et al. 2003), but can also be native species that have co-existed with humans for millennia, and so are pre-adapted to urban conditions and appreciated for their cultural significance (reviews in Hosey and Melfi 2014; Soulsbury and White 2015). Studying these synanthropic species is important for several reasons. First, they offer unique insight into the capacity of animals to withstand and even exploit human activity, thus adapting to a growingly urban world. Second, their abundance and frequent commensalism with humans makes them an integral part of the human cultural landscape, potentially making them important components of people’s sense of connection with nature (e.g. Nilon 2011; Fuller et al. 2012; Cox and Gaston 2016). Third, many of them are facultative scavengers that subsist on animal carrion and human waste, thus providing fundamental ecosystem and sanitary services, as well demonstrated in urban and rural environments (e.g. Margalida and Colomer 2012; Gangoso et al. 2013; Moleón et al. 2014; Inger et al. 2016). Fourth, they are often dominant components of the community, potentially limiting other species, and thus contributing to faunal homogenization (McKinney 2006; Shochat et al. 2010; Carey et al. 2012). Finally, these species could indicate the future behavioural and demographic characteristics of exotic urban invaders when they reach a mature stage of colonization. However, despite all the above, relatively few intensive studies have centred on these ‘synanthropic’ urban exploiters (e.g. Marzluff et al. 2001; Parker and Nilon 2012).

While research on urban ecology grows exponentially (e.g. Mayer 2010), several areas have received limited attention. In particular, there is a paucity of intensive studies conducted in tropical regions (a severe deficiency highlighted by many reviews, e.g. Chace and Walsh 2006; Magle et al. 2012; Marzluff 2016), despite the fact that urbanization will be

heavily concentrated in such areas over the coming decades (Malakoff et al. 2016). Scarce research attention has also been devoted to megacities (cities with >10 million inhabitants), most of which are themselves concentrated in developing tropical countries (Grimm et al. 2008; Malakoff et al. 2016). Furthermore, few studies have focused on facultative scavengers or top predatory species, probably because much of the urban fauna is dominated by small species with diets dominated by plant material (e.g. Evans et al. 2011). Finally, despite the obvious significance of humans to the very existence of the urban environment, remarkably few authors have either incorporated human socio-economic factors as an integral component of their ecological research (e.g. Grimm et al. 2000; Liu et al. 2007), or focused on habitat selection by individual animals, which may yield important insight into mechanisms of resilience enabling close coexistence with humans.

To contribute to these overlooked areas, we examined habitat selection by a synanthropic native top predator in the tropical megacity of Delhi, India, currently the second most populous city in the world. Here we demonstrate that its habitat choices are tightly intertwined with human activities, including specific socio-religious practices, which greatly influence the spatial distribution of food subsidies.

Methods

Model species

The Black Kite *Milvus migrans* (hereafter kite) is a medium-sized opportunistic raptor, widely distributed throughout Eurasia, Africa and Australia, and considered as the most successful raptor in the world. In India, the native, resident subspecies *M. m. govinda* is synurbic (Francis and Chadwick 2012), i.e. occurring almost exclusively in close association with humans in towns and cities (Naoroji 2006). In Delhi, kites breed on both trees and artificial structures (pylons, towers), sometimes forming loose colonies and locally reaching extremely high densities, thanks to the exploitation of human food subsidies facilitated by inefficient refuse disposal and by religious kite-feeding practices (Kumar et al. 2014; see details below). These large-scale subsidies may explain Delhi’s capacity to host what is probably the largest raptor concentration in the world (Galushin 1971; Kumar et al. 2014).

Study area

Delhi is a megacity of more than 16 million inhabitants, currently covering an area of 1500 km² and in constant, rapid expansion (Census organization of India 2011). It is polycentric and heterogeneous, with a multitude of urban

configurations, which make it difficult to establish a linear urban-rural gradient. The climate is semi-arid, with a mean annual precipitation of 640 mm, mainly concentrated in July and August during the monsoon season. Temperature ranges from a minimum mean value of 8.2 °C in the winter to a maximum mean value of 39.6 °C during the summer (Indian Metrological Department 2013). The vegetation of the general region falls within the ‘northern tropical thorn forest’ category (Champion and Seth 1968).

Two aspects of Delhi are important for kite foraging. First, large portions of the city are characterized by poor solid waste management, which affords plenty of food to kites in the form of carrion or refuse, and its associated prey-fauna (e.g. rodents, pigeons etc.). 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. These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries (Pinault 2008; Taneja 2015). Whilst meat-offering is practiced by a number of communities, in Delhi it is especially prevalent amongst members of the Muslim faith, whose numbers are concentrated in well-defined portions of the city (hereafter “Muslim colonies”). In these areas, ritualized-feeding is operated both by private individuals, and as public events, typically around mosques, where large quantities of meat are tossed to kites at predictable hours each day, sometimes causing hundreds of kites to congregate. Thus, waste management issues common to all communities, and cultural rituals which are more specific to some, generate spatial heterogeneity in the potential food availability for kites.

Field procedures

We surveyed kite nests systematically over the four years 2013–2016 at 24 plots of 1 km². These were plotted randomly within Delhi (1500 km²) so as to cover all its possible urban settings, from semi-natural to extremely built-up sites (details in Kumar et al. 2014). This resulted in a sample of 154 nests, each from a different territory, used at least once for breeding between 2013 and 2016. Nests were checked every 7–10 days until the chicks were at least 45 days old, in order to estimate the number of young raised to fledging (chicks fledge when about 48 days old; see Kumar et al. 2014 for further details of nest checks and surveys).

Breeding site characteristics

To investigate nest-site selection, we compared the urban, human and environmental variables collected at the 154 nests (see below) with those collected at an equal number of random locations, generated through ArcGIS 10.0 as follows. For each sample plot, we drew a circle of 5 km-radius centred on its

barycentre (arithmetic centre of its outline-corners, as calculated by ArcGIS 10.0) and plotted within it a number of random locations equal to the number of real nests censused in that plot (i.e. if a plot contained *X* nests, we plotted *X* random locations within its 5 km radial area). The radius of 5 km was chosen because floating, pre-breeding kites frequently prospect 7–10 km wide areas when choosing where to settle to breed (Tanferna et al. 2013; authors’ unpubl. GPS-data). Thus, we assumed that each individual could compare the habitat configuration of the location eventually chosen with potential, alternative sites within a 5 km radius, an area that would be easy to observe in its entirety by a high circling kite on a clear day. Once plotted by GIS, we: (1) visited each random location using a handheld GPS; and (2) repositioned the location on the nearest tree or artificial structure judged capable of supporting a kite nest (e.g. with a sufficiently high, solid fork, based on our previous experience in observing hundreds of kite nests).

The variables recorded at each nest or random location are detailed in Online Resource 1 Table A1, they were devised on the basis of our knowledge of local kite ecology, and measured vegetational, urban and human features at three “scales”. The “nest area” scale estimated the characteristics of the potential nesting tree or artificial structure and its immediate surroundings, such as the height of the nesting structure, woodlot size, or whether the nesting tree was isolated or in a hedgerow, parkland or woodlot (Online Resource 1, Table A1). The “landscape scale” (hereafter “urban scale”) measured the urban configuration and landscape structure within 500 m of each sample location, such as indices of road and building density, or percentage and diversity of land-cover types (Online Resource 1, Table A1). It also included the proximity to potentially important features, such as roads, water or rubbish dumps. The 500 m radius was arbitrarily chosen because this is the area around the nest most intensively patrolled for hunting by breeding individuals, especially females, based on intensive observation of focal pairs. Finally, the “human scale” provided direct and indirect estimates of human activities and practices, such as distance to Muslim colonies, efficiency of waste management, or human density. Several of these variables directly or indirectly estimated the potential access of kites to different types of human subsidies, as detailed in Online Resource 2. Nest-area characteristics were measured in the field with a metric tape. Measures of proximity and surface cover, such as distance to roads or woodlot size were assessed in Google Earth Pro and ArcGIS 10.0. Human variables, such as hygiene score or human density, were recorded through ground surveys and interviews with local people (see Online Resource 2 for details).

Statistical analyses

We used t-tests and χ^2 tests to explore differences between kite nests and random locations. We then employed a mixed

model logistic regression (Zuur et al. 2009) with a backward stepwise procedure to examine the nest-area, urban and human factors (Online Resource 1, Table A1) discriminating between kite nests and random locations. Of the total 308 available locations, we randomly selected 100 nests and 100 random sites for model building, and employed the remaining 54 nests and 54 random locations for model validation (Fielding and Haworth 1995). Because multiple nests and random locations were drawn from the same plot and its surroundings, and thus were closer to each other than those from other, more distant, sample plots, plot ID was added as a random factor.

To reduce collinearity and the number of variables presented to the logistic regression, we employed the method of variable reduction proposed by Green (1979) and commonly employed in habitat selection studies (e.g. Austin et al. 1996; Soh et al. 2002). In this method, pairs of strongly inter-correlated variables ($r > 0.60$) are considered as estimates of a single underlying factor, and only one of the two is retained for analysis, usually the one likely to be perceived as more important by the study organism. Collinearity was subsequently checked further by examining the variance inflation factors (VIF) of the explanatory variables, which were always low (< 2 ; Crawley 2007; Zuur et al. 2009).

Some of the kites of our study population were GPS-tagged as part of a parallel study on their movement ecology. Because these individuals visited multiple Muslim colonies, and because large numbers of kites (e.g. > 100) were seen to assemble during ritual-feeding episodes, suggesting congregation from distant sites, we decided to estimate the distance of each nest or random location from multiple Muslim colonies. When we compared such distances between nests and random points in exploratory analyses, kites seemed to over-select sites closer than available to the 1st, 2nd and, possibly, 3rd closest colony, after which the difference became unimportant (Online Resource 3). Thus, to provide a comprehensive measure that integrated the proximity to the three nearest Muslim colonies with their human population density (under the assumption that higher rates of refuse and ritualized-feeding should occur in denser colonies), we extracted the first component of a PCA (Tabachnick and Fidell 1996) run on these four aforementioned variables. Its PC1 (hereafter “access to Muslim subsidies”) explained 65% of the variance and had a high positive loading on Muslim population density and high negative loadings on the distance to the 1st, 2nd and 3rd closest Muslim colonies. Thus, it provided an increasing index of access to abundant “Muslim subsidies” and was fitted to all models (Online Resource 1, Table A3).

To gain a deeper understanding of habitat quality available to kites, and to test whether the observed habitat choices were adaptive (e.g. Clark and Schutler 1999; Sergio et al. 2003), we used linear mixed models. These again used plot ID as a random factor and tested the effect of the same set of variables presented

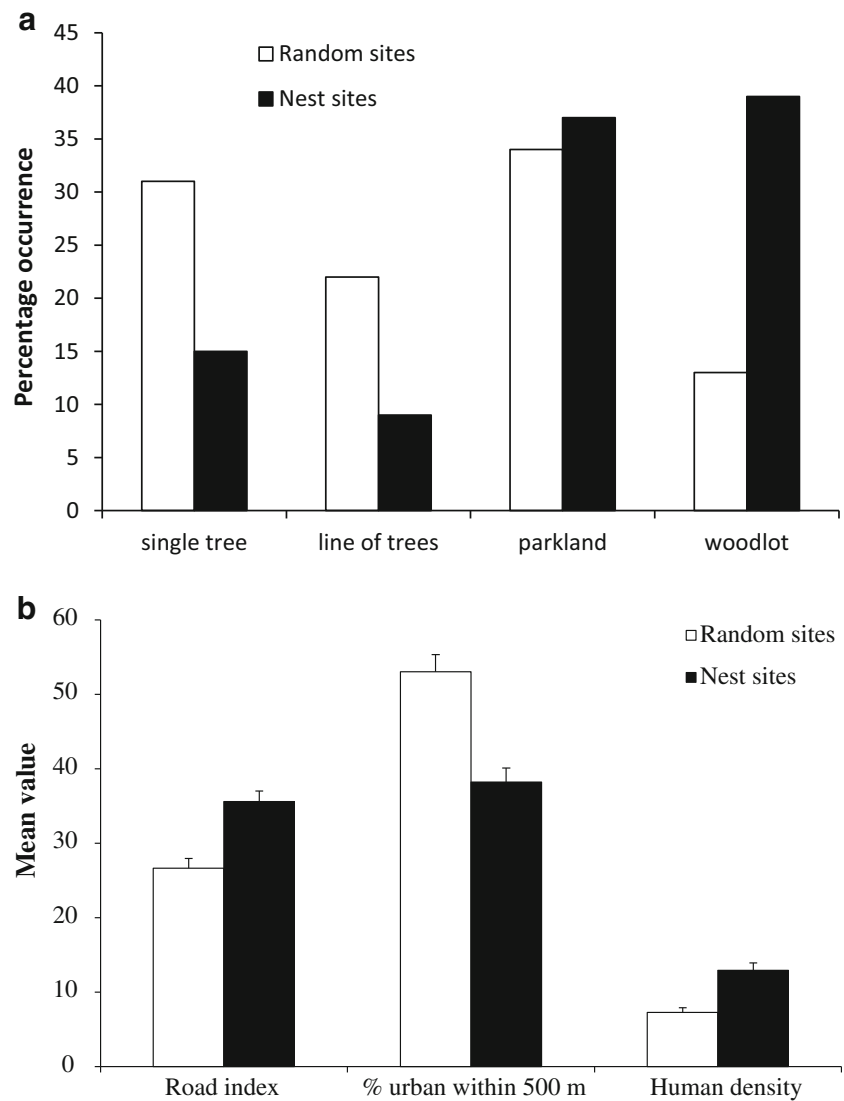
to the habitat selection logistic model on both the number of years that a territory was occupied and on the cumulative number of fledglings that it produced between 2013 and 2016. We predict that territories that were more frequently occupied were of higher quality and thus were more attractive to kites, as has been demonstrated in other avian species, including other kite populations (review in Sergio and Newton 2003).

All multivariate models were built by a frequentist approach through a backward stepwise procedure following Zuur et al. (2009): all explanatory variables were fitted to a maximal model, extracted one at a time from the maximal model, 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 (Zuur et al. 2009). To avoid over-parameterization, we ensured never to fit more than $N/3$ variables to each maximal model, where N is the sample size of the analyzed dataset (Crawley 2007). Interactions were fitted only when we had a priori hypotheses about their potential effect, based on our field observations and knowledge of the population. In particular, we hypothesized that the selection of green cover, urban cover or hygiene level could be conditional upon proximity to Muslim subsidies, because the latter could affect habitat and food profitability. We also hypothesized that the preference for a low level of hygiene (i.e. for high human waste availability) could depend on human density and vice versa, and thus fitted the interaction between hygiene score and human density. Model assumptions were checked by investigating QQ plots, histograms of residuals, and plots of standardized and normalized residuals against fitted values and against explanatory variables (Crawley 2007; Zuur et al. 2009). All GLMMs were implemented in R.3.0.2 (R Development Core Team 2009). When necessary, variables were logarithmically, or arc-sine square root transformed in order to achieve a normal distribution. All tests are two-tailed, statistical significance was set at $\alpha < 0.05$, and all means are given ± 1 SE.

Results

In univariate tests (Online Resource 1, Table A2), at the nest-area scale, kites did not prefer trees over artificial structures, although most nests (87%) were built in trees. There was also no clear preference for tree species, with kites opportunistically using 13 different tree species (Online Resource 4). Instead, they seemed more selective of the arrangement of trees, over-selecting woodlots and parklands rather than single trees or lines of trees (Fig. 1a). Also, when they nested in woodlots, they selected larger woodlots than the average available (Online Resource 1, Table A2). At the urban scale, kites preferred sites with lower human housing densities, lesser extents of built-up surfaces, higher availability of roads and woodland,

Fig. 1 Tree arrangement (Panel **a**), and index of road density, percentage urban land cover within a 500 m radius, and human density (panel **b**) at 100 Black Kite nests (black bars) and 100 random locations (white bars) in Delhi (India)



and higher habitat diversity (Online Resource 1, Table A2). Finally, kite nests differed from random locations for all human variables. Compared to availability, nests had higher access to Muslim subsidies, higher density of Muslim inhabitants, higher human density in the streets and greater quantities of anthropogenic refuse (Online Resource 1, Table A2).

According to the logistic model discriminating between kite nests and random locations (Online Resource 1, Table A3a), kites preferentially selected sites in woodland, with higher road density, with less urban cover and greater woodland extent at the landscape scale, with higher human densities in the streets, lower hygiene levels and greater access to Muslim subsidies (Fig. 1a, b; 2b). The interaction of access to Muslim subsidies with hygiene

score and with woodland land-cover also entered the model (Online Resource 1, Table A3a): first, low-refuse sites were selected if found close to Muslim colonies, while locations with much refuse were over-selected when far from Muslim subsidies (Fig. 3). Second, large woodland extents were preferred close to Muslim colonies but avoided when far from them (Fig. 2a, b). The logistic model performed well when reapplied on both the training and validation datasets: it correctly reclassified 87% of the 200 locations used for model building (87% of 100 nests and 87% of 100 random sites), and 82% of the 108 locations set apart for validation (97.4% of 54 nests and 74.1% of 54 random sites).

Finally, both territory occupancy and breeding output were higher for territories with higher access to Muslim

subsidies, and for those located in parkland and woodland (Online Resource 1, Table A3b, c).

Discussion

Our study offers a clear example of cities as complex ecosystems that link society and biota at multiple spatio-temporal scales. In particular, integrating human activities and practices with ecological processes at vast spatial scales allowed us to investigate resources which would have otherwise been missed by conventional ecological analyses of urban land-cover. This reinforces the call for improved integration of socio-economic approaches to urban ecology, which will often require a reconceptualization of humans and their activities (Pickett et al. 2001; Grimm et al. 2008; Esbjorn-Hargens and Zimmerman 2009; Warren and Lepczyk 2012). Furthermore, the high predictive power of our logistic model of nest-site selection highlighted the importance of habitat models as potential conservation tools for urban planning (for integration of modelling and conservation in urban settings, see examples and reviews in Gordon et al. 2009; Kowarik 2011; Lepczyk and Warren 2012; Lerman et al. 2014).

Overall, our model suggested that Delhi Black Kites selected several socio-ecological features at multiple scales, from local tree-arrangement, to neighbourhood-level landscape structure, to the larger-scale spatial zoning of access to subsidies provided by human socio-religious practices (see below). Thus, the city was not homogenous in its suitability for kites, as might be assumed from their apparently constant presence throughout the city (e.g. Galushin 1971), which is typical of many facultative scavengers and synurbic species capable of consuming human waste (e.g. Sorace 2002; Brook et al. 2003). On the contrary, kites avoided monotonously built-up portions of the city and over-selected sites according to the following, very specific urban template.

First, our model suggested that, compared to availability, kites over-selected woodland patches and avoided isolated trees or lines of trees. Woodlots may allow a more favourable micro-climate in a hot tropical city (e.g. Wang et al. 2015). They may also provide higher nest-site availability and thus accommodate a loose kite colony, with consequent potential advantages in turn of conspecific cuing to locate food (e.g. Valone and Templeton 2002; Danchin et al. 2004), likely to be important in this species (Sergio 2003; Sergio and Penteriani 2005) and in this population in particular (see below). The fact that the rate of selection increased from single trees (strongly avoided), to lines of trees (moderately avoided), to parkland (used as available) and then woodland (Fig. 1a) conforms to a progression of attraction to structural arrangements facilitating increasing levels of conspecific proximity. A preference for large patches of parkland and woodland has previously been demonstrated for other raptors

inhabiting urban areas (e.g. Hogg and Nilon 2015; McPherson et al. 2016; Morrison et al. 2016) and confirms the importance of the abundance and arrangement of green vegetation for urban biota (Lepczyk et al. 2017).

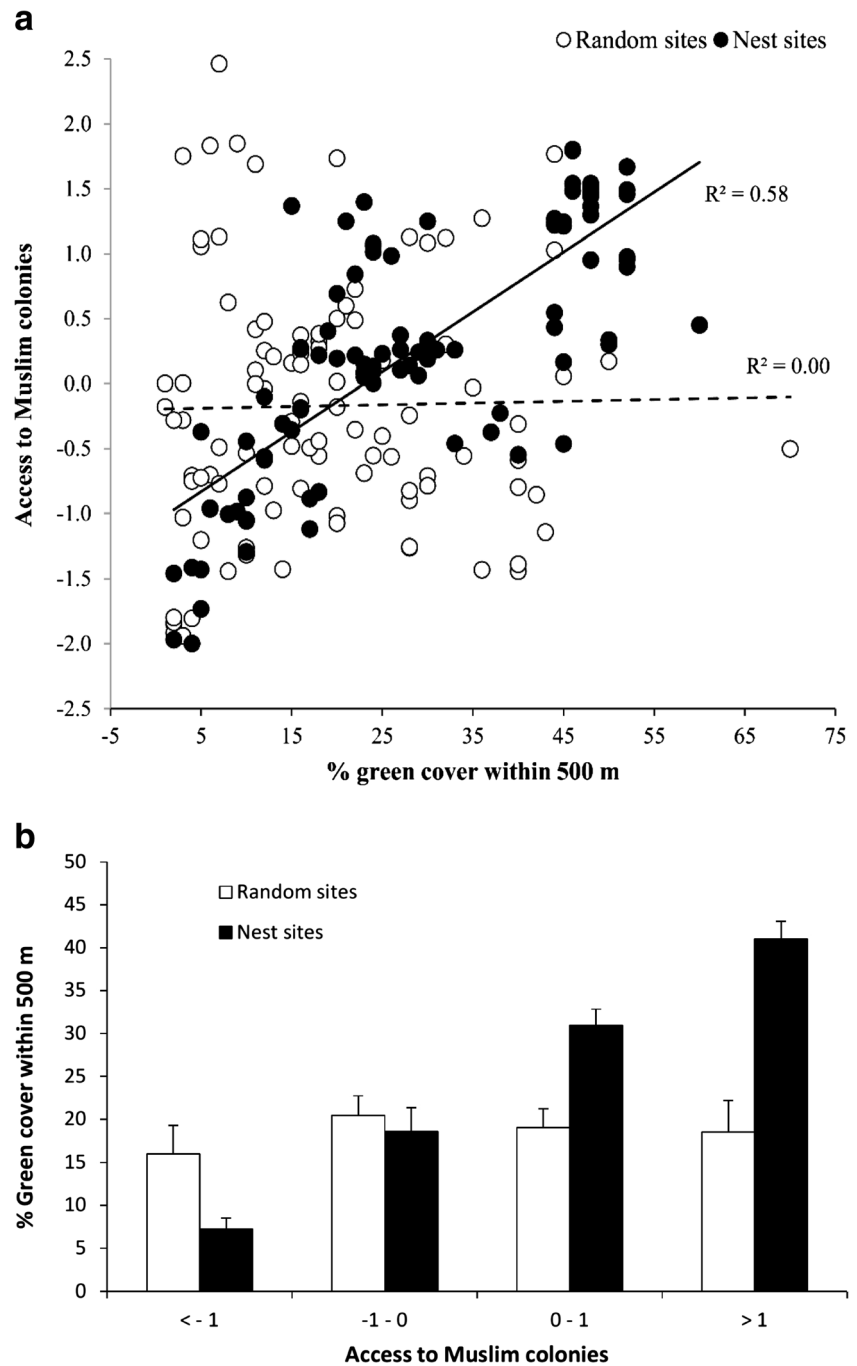
Second, while kites avoided high rates of built-up land cover, they simultaneously selected areas with high road and human density. Because human density was assessed in the streets, it equated to an index of human traffic and street-activity, and because refuse is often disposed of by people in a disorganized and unpredictable manner in Delhi, high levels of human activity in the streets likely implies more waste accumulation in these areas. This may provide food directly for kites or for co-occurring species that may in turn represent live prey for kites, such as small mammals or pigeons. Thus, kite's habitat decisions seemed to be set not simply on human density per se, which would probably be higher in densely built-up areas (actually avoided), but more specifically on a high density of roads with intense human activity. In this sense, urban configuration was important as it 'structurally' mediated the kites' access to the functionally relevant portion of the human population. In agreement with this interpretation, we have frequently observed hunting kites quartering over roads, or moving through a series of dominant perches, intently 'observing' human traffic in the streets below. Furthermore, the kites' preference for neighbourhoods with less efficient waste management further reinforced the idea that the link with human street-activities was ultimately aimed at refuse exploitation. These analyses confirm the need to integrate conventional variables describing the urban landscape with more direct measures of human activities and practices, as highlighted by various authors (e.g. Alberti 2008; Pickett et al. 2001; Grimm et al. 2008; Warren and Lepczyk 2012).

Third, kites over-selected sites that allowed ready access to multiple Muslim colonies, i.e. to concentrations of people whose activities increased the availability of easy food. While several previous studies have investigated the effect of human subsidies on urban taxa, they have usually focused on garden-feeding operated by citizens of the northern hemisphere as a leisure activity (e.g. Fuller et al. 2012; Lepczyk et al. 2012; Cox and Gaston 2016). In our case, the spatial association of ritualized-feeding with certain religious communities completed the picture of these previous studies by adding a further socio-cultural component, which strongly characterizes the urban settings of large portions of southern Asia (see also Keniger et al. 2013). In our specific case, the ritual of tossing meat to kites, which is a widespread practice operated daily at predictable public sites, especially among members of the Muslim communities, has probably generated a mosaic of patches with high input of human subsidies. In agreement with this, our GPS-tagged kites regularly visited these sites with very deliberate-directed journeys to them and large numbers of kites, sometimes into the hundreds, were regularly seen to gather quickly during ritual-feeding

episodes. However, this high level of congregation may also enhance competition, lowering the predictability of successful access to the subsidy at the individual kite level. This may explain the preference for proximity to multiple Muslim colonies, each one with multiple ritual-feeding sites, as this will allow each individual dozens of daily opportunities to access subsidies. Furthermore, strategic positioning of the nest within 1–2 km of multiple Muslim colonies may allow kites to spot flocks of conspecifics exploiting feeding-rituals, which are conspicuous even to humans, and to join them rapidly through

conspecific cueing, as reported for kites in more natural environments (e.g. Sergio 2003). Note that the ability to exploit sudden flushes of easy food is one of the defining characteristics of this highly opportunistic species even in rural settings (Blanco 1997; Viñuela 2000), an ability which may have further pre-adapted it to life in a megacity. The above described coincidence of resource predictability, opportunism, high sociality, and high visibility of conspecific behaviour represents a typical scenario for the evolution of behavioural strategies based on conspecific cueing and attraction (e.g. Valone and

Fig. 2 Urban kites in Delhi selected sites for which access to Muslim colonies and vegetation cover positively covaried (panel **a**). Thus, they over-selected areas with abundant vegetation close to dense Muslim colonies, but avoided them when far from Muslim colonies (panel **b**). Access to Muslim colonies was estimated by means of a principal component analysis (see Methods) and portrayed as a categorical progression in panel **b** for clarity of presentation. Error bars represent 1 SE, black points/bars portray kite nests and white points/bars represent random locations



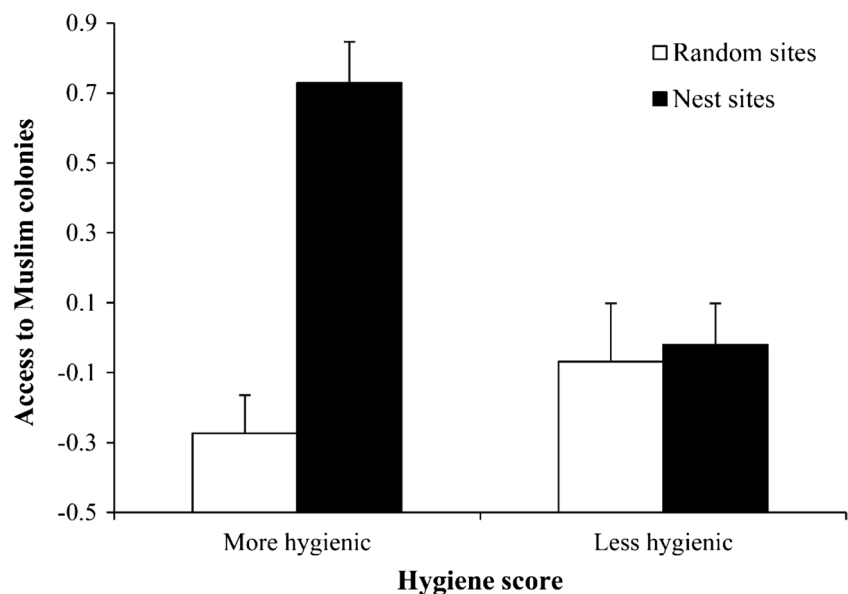
Templeton 2002; Danchin et al. 2004). The advantages described above were confirmed by the higher occupation rate and breeding output of territories in proximity to multiple Muslim colonies, which suggested that these sites were attractive to kites, that they contributed a disproportionate number of fledglings to the population, and that the observed habitat choices were adaptive in terms of offspring production (i.e. over-selection of sites which offer a reproductive reward).

Fourth, the importance of strategic proximity to Muslim colonies was further confirmed by its interaction with other habitat features. Compared to a random distribution, kites over-selected sites for which green cover and access to Muslim colonies covaried positively (Fig. 2a). This implied that, close to Muslims, kites preferred neighbourhoods with abundant green cover, which may accommodate more nests and facilitate colony-formation, with potential benefits in terms of conspecific cueing (e.g. being alerted of the start of feeding-rituals by the departure of nearby conspecifics). Ultimately, this should allow density to be fine-tuned on food availability (larger densities close to large food concentrations). On the contrary, in scenarios of low food availability (low access to Muslim colonies, Fig. 2b), kites preferred sites with low green cover, which will limit density, thus lowering competition for limited food. Furthermore, the preference for proximity to Muslim colonies was especially pronounced in neighbourhoods where human refuse was scarce (Fig. 3). When hygiene levels were already low, food was likely available in the immediate nest surroundings, allowing kites to be less dependent on Muslim colonies and to nest farther from them. These results suggest that (a) access to hotspots of ritualized-feeding modulated the suitability of other habitats, even when these were located kilometres away from such sites, which functionally integrated far-away components of the urban ecosystem (see also Grimm et al. 2000; Alberti 2008); (b) ritualized subsidies and waste production/disposal seemed to be the two pillars

that directly or indirectly permeated all habitat preferences; and (c) kites seemed to strategically balance their access to these two factors in their habitat choices.

Overall, kite habitat decisions were tightly intertwined with human activities. They preferred sites with extensive access to roads busy with humans, with inefficient waste management and ready access to ritual cultural practices conducive to food subsidies. To date, humans have often been seen as obstacles, threats or nuisances that animal species have to deal with in order to ‘tolerate’ urbanization (e.g. Soh et al. 2002; Chace and Walsh 2006; McPherson et al. 2016). However, for many urban species, the attraction to an extreme anthropogenic ecosystem is based on the exploitation of human provision itself rather than resilience to its actions, and for some synanthropic species this may derive from millennia of co-existence with man, better seen as an integral portion of their niche as well as a beneficiary of ecosystem services (e.g. Marzluff and Angell 2005; Gangoso et al. 2013). In our system, Delhi kites cannot be thought of in isolation from humans and their voluntary and involuntary subsidies, which would qualify them as anthropophilic and anthropodependent species (sensu Hulme-Beaman et al. 2016). While the importance of human subsidies in altering the mosaic of foraging opportunities for animals is well appreciated (Fuller et al. 2012; Lepczyk et al. 2012; Oro et al. 2013; Newsome et al. 2014), in our case the subsidy-mosaic was uniquely tied to a complex array of human themes, such as (1) the Indian-level and local-level history of Muslim displacements, which followed India’s independence and which determined the current distribution of Muslim colonies; (2) the global economy that drives urban sprawl, as well as the local economics of trade, which influenced the stability of some historical Muslim colonies; (3) the municipal planning of the currently skyrocketing urban expansion, which affects road and vegetation arrangement, as

Fig. 3 Access to dense Muslim colonies was higher at Black Kite nests (black bars) than at random locations (white bars) when local hygiene levels were high, while inefficient refuse disposal (i.e. low local hygiene) “released” kites from dependency on Muslim ritual subsidies. Error bars represent 1 SE



well as the efficiency of refuse disposal; and (4) the temporal dynamicity of cultural and religious practices, such as ritualized-feeding, which originated among Hindus but is currently prevalent among Muslim groups (e.g. Gupta 1998; Pinault 2008; Sharan 2014; Paul and Nagendra 2015; Taneja 2015). All the above tied kites' habitat choices to the spatial end-results of human activities shaped by history, socio-economics, politics, tradition and religion. Also, these links acted at time scales ranging from decades to centuries and at spatial scales ranging from neighbourhood to global. We believe that similarly tight and complex relations will apply to many other synurbic species worldwide (Francis and Chadwick 2012).

Conservation implications

The preference for certain amounts and configurations of woodland makes room for potential modulation of kite density through urban planning, as proposed for crows in Singapore (Soh et al. 2002). For example, promotion of woodlots close to areas with problematic refuse disposal may improve the potential ecological service provided by kite consumption of organic waste, a benefit that could be confirmed through adaptive management. Over the longer-term, waste disposal will be likely rationalized, mechanized and often processed indoor, as progressively legally enforced in developed countries. This will likely imply major declines in kite food availability, which could be partly buffered by planned maintenance and promotion of ritual feeding practices, seen as a unique connection between human culture and ecological function in rapidly expanding urban ecosystems (see below).

The close connection of urban kites to human activities, and their wide-ranging behaviour, typical of mobile avian predators, which tied them to far away sectors of the city, make them an ideal indicator species that integrates processes occurring at different scales of the urban landscape. In particular, the dependency of an urban top predator on ritual feeding, human culture and religion, which promotes one of the largest predator concentrations in the world (Kumar et al. 2014), could be seen as a socio-cultural and ecological uniqueness that connects urban dwellers with nature and has to be attentively preserved, just as an urban green space. In this context, investigation and documentation of the socio-historical aspects and ecological implications of ritual feeding should be actively promoted.

As any megacity, Delhi is likely to change rapidly in coming decades in terms of sprawl, internal structure, management and culture (Grimm et al. 2008; Sharan 2014; Srivastava 2015). Modernization will sooner or later rationalize refuse disposal and younger generations already seem less interested in cultural practices such as ritualized-feeding (authors unpubl. Data), which will imply major shifts in resource availability and a threat to a unique system of human-predator coexistence.

Such conundrums between modernization, improving human conditions and protecting unique eco-cultural treasures such as the ritual feeding of kites will be formidable challenges to urban planning for innumerable, fast-growing towns and cities of the developing world (e.g. Gangoso et al. 2013).

Acknowledgements We thank Prof. Nilon and two anonymous reviewers for constructive comments on an earlier draft of the manuscript. We are grateful to Ben Sheldon, Chris Perrins, Tommaso Pizzari, Ujjwal Kumar, L. Agarwal and the Director, Dean and research coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. Delhi Police, and the Forest Departments of Delhi and Uttar Pradesh, Civic bodies of the Government of NCT of Delhi helped with legal permits, and Mr. A. Agnihotri, Director of the National Zoological Park of New Delhi provided accommodation and gave permission to study kites in the Park. Miranda House College and University of Delhi allowed access to their campus for nest monitoring. We express our most heartfelt gratitude to N. Shehzad and M. Saud of Wildlife Rescue for providing essential information, and to all the volunteers of the “Black Kite Project Group” from the University of Delhi (Sri Venkateswara and Deshbandhu Colleges), especially R. Prajapati, R. Negi, B. Sharma, P. Kumar and M. Singh who provided essential field help, enthusiasm and cooperation in the environmental education of locally assembling crowds of curious people. Special thanks to our field assistant Laxmi Narayan, who was the backbone of the field team. Finally, thanks to all the landowners, managers and government officials who patiently cooperated with our constant requests of access. The project was funded through grants by the Raptor Research and Conservation Foundation (Mumbai) and by the Govt. of India, Ministry of Environment, Forest and Climate Change. N Kumar's D. Phil at the University of Oxford was funded by the Felix Scholarship Trust. Funding for travelling and fieldwork by F. Sergio was afforded by Project RNM-7307 of the Junta de Andalucía and CGL2015- 69445-P of the Spanish Ministry of Economy and Competitiveness.

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References

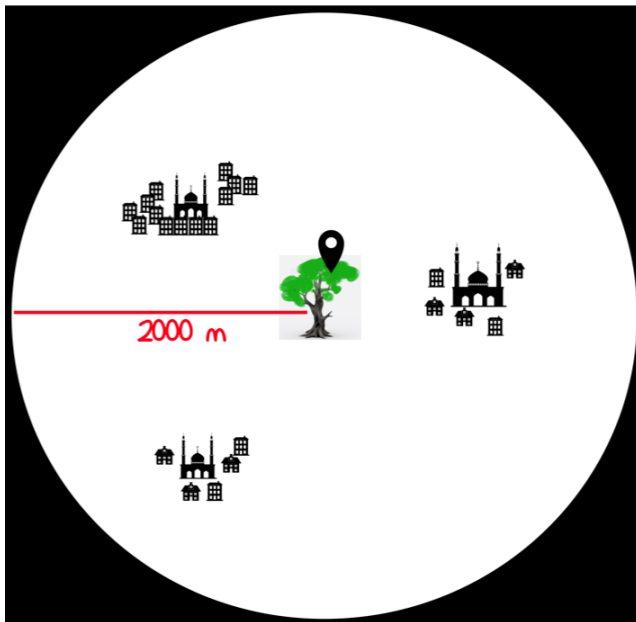
- Alberti M (2008) Advances in urban ecology: integrating humans and ecological processes in urban ecosystems. Springer, New York. <https://doi.org/10.1007/978-0-387-75510-6>
- Anonymous (2016) Rise of the city. *Science* 352:906–907
- Austin GE, Thomas CJ, Houston DC, Thompson BA (1996) Predicting the spatial distribution of buzzards *Buteo buteo* nesting areas using a geographical information system and remote sensing. *J Appl Ecol* 33(6):1541–1550. <https://doi.org/10.2307/2404792>
- Belant JL (1997) Gulls in urban environments: landscape-level management to reduce conflict. *Landsc Urban Plan* 38(3–4):245–258. [https://doi.org/10.1016/S0169-2046\(97\)00037-6](https://doi.org/10.1016/S0169-2046(97)00037-6)
- Blanco G (1997) Role of refuse as food for migrant, floater and breeding black kites (*Milvus migrans*). *Journal of Raptor Research* 31:71–76
- Brook BW, Sodhi NS, Soh NCK, Chuam Lim H (2003) Abundance and projected control of invasive house crows in Singapore. *J Wildl Manag* 67(4):808–817. <https://doi.org/10.2307/3802688>
- Carey MP, Sanderson BL, Barnas KA, Olden JD (2012) Native invaders: challenges for science, management, policy, and society. *Frontiers in. Ecol Environ* 10(7):373–381. <https://doi.org/10.1890/110060>

- Census organization of India (2011) Census of India. <http://censusindia.gov.in/2011census>. Accessed 25 February 2017
- Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. *Landsc Urban Plan* 74(1):46–49. <https://doi.org/10.1016/j.landurbplan.2004.08.007>
- Champion HG, Seth SK (1968) A revised survey of the Forest types of India. Manager of Publications, Government of India, New Delhi
- Clark RG, Schutler D (1999) Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology* 80(1):272–287. [https://doi.org/10.1890/0012-9658\(1999\)080\[0272:AHSPFP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[0272:AHSPFP]2.0.CO;2)
- Cox DTC, Gaston KJ (2016) Urban bird feeding: connecting people with nature. *PLoS One* 11(7):e0158717. <https://doi.org/10.1371/journal.pone.0158717>
- Crawley MJ (2007) The R book. Wiley Press, Chichester. <https://doi.org/10.1002/9780470515075>
- Danchin É, Giraldeau L, Valone TJ, Wagner RH (2004) Public information: from noisy neighbors to cultural evolution. *Science* 305(5683):487–491. <https://doi.org/10.1126/science.1098254>
- Esbjorn-Hargens S, Zimmerman ME (2009) Integral ecology: uniting multiple perspectives on the natural world. Integral Books, Boston
- Evans KL, Chamberlain DE, Hatchwell BJ, Gregory RD, Gaston KJ (2011) What makes an urban bird? *Glob Chang Biol* 17(1):32–44. <https://doi.org/10.1111/j.1365-2486.2010.02247.x>
- Fielding AH, Haworth PF (1995) Testing the generality of bird-habitat models. *Conserv Biol* 9(6):1466–1481. <https://doi.org/10.1046/j.1523-1739.1995.09061466.x>
- Francis RA, Chadwick MA (2012) What makes a species synurbic? *Appl Geogr* 32(2):514–521. <https://doi.org/10.1016/j.apgeog.2011.06.013>
- Fuller RA, Irvine KN, Davies ZG, Armsworth PR, Gaston KJ (2012) Interactions between people and birds in urban landscapes. *Avian Biology* 45:249–266
- Galushin VM (1971) A huge urban population of birds of prey in Delhi India. *Ibis* 113:522
- Gangoso L, Agudo R, Anadón JD, dela Riva M, Suleyman AS, Porter R, Donázar JA (2013) Reinventing mutualism between human and wild fauna: insights from vultures as ecosystem services providers. *Conserv Lett* 6(3):172–179. <https://doi.org/10.1111/j.1755-263X.2012.00289.x>
- Gordon A, Simondson D, White M, Moilanen A, Bekessy SA (2009). Integrating conservation planning and landuse planning in urban landscapes. *Landsc Urban Plan* 91(4):183–194. <https://doi.org/10.1016/j.landurbplan.2008.12.011>
- Green RH (1979) Sampling design and statistical methods for environmental biologists. John Wiley and Sons, New York
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and ecology of cities. *Science* 319(5864):756–760. <https://doi.org/10.1126/science.1150195>
- Grimm NB, Steward JMG, Pickett TA, Redman CL (2000) Integrated approaches to long-term studies of urban ecosystems. *Bioscience* 50(7):571–584. [https://doi.org/10.1641/0006-3568\(2000\)050\[0571:IATLTO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0571:IATLTO]2.0.CO;2)
- Gupta N (1998) Delhi between two empires, 1803–1931: society, government, and urban growth. Oxford University Press, New Delhi
- Hogg JR, Nilon CH (2015) Habitat associations of birds of prey in urban business parks. *Urban Ecosyst* 18(1):267–284. <https://doi.org/10.1007/s11252-014-0394-8>
- Hosey G, Melfi V (2014) Human-animal interactions, relationships and bonds: a review and analysis of the literature. *Int J Comp Psychol* 27:117–142
- Hulme-Beaman A, Dobney K, Cucchi T, Searie JB (2016) An ecological and evolutionary framework for commensalism in anthropogenic environments. *Trends Ecol and Evol* 31(8):633–645. <https://doi.org/10.1016/j.tree.2016.05.001>
- Indian Metrological Department (2013) <http://amssdelhi.gov.in/climatology/sfd1.htm>. Accessed 27 January 2017
- Inger R, Cox DTC, Per E, Norton BA, Gaston KJ (2016) Ecological role of vertebrate scavengers in urban ecosystems in the UK. *Ecol Evol* 19:7015–7023
- Keniger LE, Gaston KJ, Irvine KN, Fuller RA (2013) What are the benefits of interacting with nature? *J Environ Res Public Health* 10:913–935
- Kowarik I (2011) Novel urban ecosystems, biodiversity, and conservation. *Environ Pollut* 159(8–9):1974–1983. <https://doi.org/10.1016/j.envpol.2011.02.022>
- 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):1–8. <https://doi.org/10.1080/00063657.2013.876972>
- Kurosawa R, Kanai Y, Matsuda M (2003) Conflict between human and crows in greater Tokyo. *Global. Environ Res* 7:139–147
- Lepczyk CA, Aronson MFJ, Goddard MA, Lerman SB, MalIvor JS (2017) Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. *Bioscience* 67(9):799–807. <https://doi.org/10.1093/biosci/bix079>
- Lepczyk CA, Warren PS (2012) Urban bird ecology and conservation. University of California Press, Berkeley. <https://doi.org/10.1525/california/9780520273092.001.0001>
- Lepczyk CA, Warren PS, Machabée L, Kinzig AP, Mertig AG (2012) Who feeds the birds? A comparison across regions. In: Lepczyk CA, Warren PS (eds) Urban bird ecology and conservation. University of California Press, Berkeley, pp 267–286. <https://doi.org/10.1525/california/9780520273092.003.0017>
- Lerman SB, Nislow KH, Nowak DJ, DeStefano S, King DI, Jones-Farrand T (2014) Using urban forest assessment tools to model bird habitat potential. *Landsc Urban Plan* 122:29–40. <https://doi.org/10.1016/j.landurbplan.2013.10.006>
- Liu J et al (2007) Complexity of coupled human and natural systems. *Nature* 31:1513–1516
- Magle SB, Hunt VM, Vernon M, Crooks KR (2012) Urban wildlife research: past, present, and future. *Biol Conserv* 155:23–32. <https://doi.org/10.1016/j.biocon.2012.06.018>
- Malakoff D, Wigginton NS, Fahrenkamp-Uppenbrink J, Wible B (2016) Rise of the urban planet. <http://www.sciencemag.org/news/2016/05/rise-urban-planet>. Accessed 12.10.16
- Margalida A, Colomer MA (2012). Modelling the effects of sanitary policies on European vulture conservation. *Sci Rep* 2:753. <https://doi.org/10.1038/srep00753>
- Marzluff JM (2016) A decadal review of urban ornithology and a prospectus for the future. *Ibis* 159:1–13
- Marzluff JM, Angell T (2005) Cultural coevolution: how human bond with crows and ravens extends theory and raises new questions. *J Ecol Anthropol* 9(1):69–75. <https://doi.org/10.5038/2162-4593.9.1.5>
- Marzluff JM, McGowan KJ, Donnelly R, Knight RL (2001) Causes and consequences of expanding American crow populations. In *Avian ecology and conservation in an urbanizing world* (Eds. J.M. Marzluff, R. Bowman, R. Donnelly), pp. 331–363. Kluwer Academic, Norwell
- Mayer P (2010) Urban ecosystems research joins mainstream ecology *Nature*: 467: 153, Urban ecosystems research joins mainstream ecology, 7312. <https://doi.org/10.1038/467153b>
- McKinney ML (2010) Urbanization, biodiversity, and conservation. *Bioscience* 52:883–890
- McKinney ML (2006) Urbanization as a major cause of biotic homogenization. *Biol Conserv* 127(3):247–260. <https://doi.org/10.1016/j.biocon.2005.09.005>
- McPherson SC, Brown M, Downs CT (2016) Crowned eagle nest sites in an urban landscape: requirements of a large eagle in the Durban metropolitan open space system. *Landsc Urban Plan* 146:43–50. <https://doi.org/10.1016/j.landurbplan.2015.10.004>

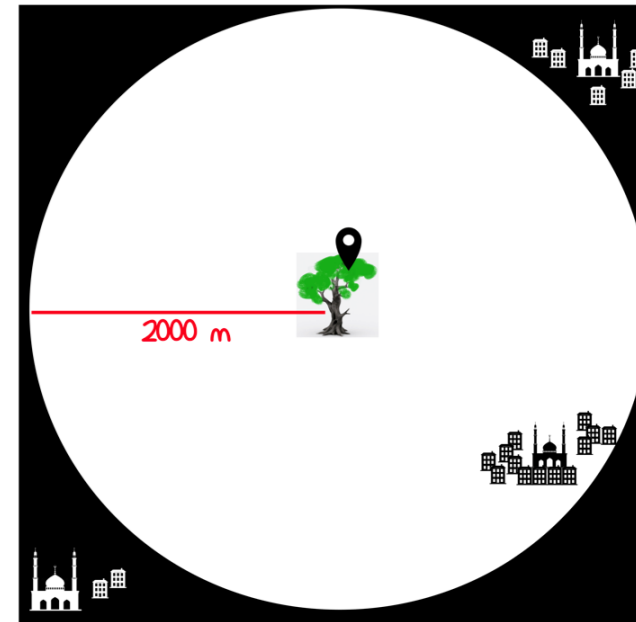
- Moleón M, Sánchez-Zapata JA, Margalida A, Carrete M, Owen-Smith N, Donazar JA (2014) Humans and scavengers: the evolution of interactions and ecosystem services. *Bioscience* 64(5):394–403. <https://doi.org/10.1093/biosci/biu034>
- Morrison JL, Gottlieb IGW, Pias KE (2016) Spatial distribution and the value of green spaces for urban red-tailed hawks. *Urban Ecosyst* 19(3):1373–1388. <https://doi.org/10.1007/s11252-016-0554-0>
- Naorji R (2006) Birds of prey of the Indian subcontinent. Christopher Helm/AandC Black Publishers Ltd., London
- Newsome TM, Dellinger JA, Pavey CR, Ripple WJ, Shores CR, Wirsing AJ, Dickman CR (2014) The ecological effects of providing resource subsidies to predators. *Glob Ecol Biogeogr* 24:1–11
- Nilon CH (2011) Urban biodiversity and the importance of management and conservation. *Landsc Ecol Eng* 7(1):45–52. <https://doi.org/10.1007/s11355-010-0146-8>
- Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A (2013) Ecological and evolutionary implications of food subsidies from humans. *Ecol Lett* 16(12):1501–1514. <https://doi.org/10.1111/ele.12187>
- Parker TS, Nilon CH (2012) Urban landscape characteristics correlated with the synurbization of wildlife. *Landsc Urban Plan* 106(4):316–325. <https://doi.org/10.1016/j.landurbplan.2012.04.003>
- Paul S, Nagendra H (2015) Vegetation change and fragmentation in the mega city of Delhi: mapping 25 years of change. *Appl Geogr* 58:153–166. <https://doi.org/10.1016/j.apgeog.2015.02.001>
- Pickett STA, Cadenasso ML, Grovem JM, Nilon CH, Pouyat RV, Zipperer WC, Costanza R (2001) Urban ecological systems: linking terrestrial, ecological, physical, and socioeconomic components of metropolitan areas. *Annual Review of Ecology Evolution and Systematics* 32(1):127–157. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114012>
- 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. Paneault). Equinox Publishing Ltd, Bristol, pp 108–121
- R Development Core Team (2009) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. URL <http://www.R-project.org>. Accessed 27 Dec 2016
- Sergio F (2003) From individual behavior to population pattern: weather-dependent foraging and breeding performance in black kites. *Anim Behav* 66(6):1109–1117. <https://doi.org/10.1006/anbe.2003.2303>
- Sergio F, Newton I (2003) Occupancy as a measure of territory quality. *J Anim Ecol* 72(5):857–865. <https://doi.org/10.1046/j.1365-2656.2003.00758.x>
- Sergio F, Pedrini P, Marchesi L (2003) Spatio-temporal shifts in gradients of habitat quality for an opportunist avian predator. *Ecography* 26(2):243–255. <https://doi.org/10.1034/j.1600-0587.2003.03426.x>
- Sergio F, Penteriani V (2005) Public information and territory establishment in a loosely colonial raptor. *Ecology* 86(2):340–346. <https://doi.org/10.1890/04-0137>
- Sharan A (2014) In the city, out of place: nuisance, pollution, and dwelling in Delhi, c. 1850–2000. Oxford University Press, Oxford. <https://doi.org/10.1093/acprof:oso/9780198097297.001.0001>
- Shochat E, Lerman SB, Anderies JM, Warren PS, Faeth SH, Nilon CH (2010) Invasion, competition, and biodiversity loss in urban ecosystems. *Bioscience* 60(3):199–208. <https://doi.org/10.1525/bio.2010.60.3.6>
- Soh MCK, Sodhi NS, Seoh RKH, Brook BW (2002) Nest site selection of the house crow (*Corvus splendens*), an urban invasive bird species in Singapore and implications for its management. *Landsc Urban Plan* 59(4):217–226. [https://doi.org/10.1016/S0169-2046\(02\)00047-6](https://doi.org/10.1016/S0169-2046(02)00047-6)
- Sorace A (2002) High density of bird and pest species in urban habitats and the role of predator abundance. *Ornis Fennica* 79:60–71
- Soulsbury CD, White PCL (2015) Human-wildlife interactions in urban areas: a review of conflicts, benefits and opportunities. *Wildl Res* 42(7):541–553. <https://doi.org/10.1071/WR14229>
- Srivastava S (2015) Entangled urbanism: slum, gated community and shopping all in Delhi and Gurgaon. Oxford University Press, Oxford
- Tabachnick BG, Fidell LS (1996) Using multivariate statistics. HarperCollins, New York
- Taneja AV (2015) Sainly animals: the shifting moral and ecological landscapes of North India. *Comparative Studies of South Asia, Africa and the Middle East* 35(2):204–221. <https://doi.org/10.1215/1089201x-3138988>
- Tanfema A, López-Jimenez L, Blas J, Hiraldo F, Sergio F (2013) Habitat selection by black kite breeders and floaters: implications for conservation management of raptor floaters. *Biol Conserv* 160:1–9. <https://doi.org/10.1016/j.biocon.2012.12.031>
- United Nations (2014) World urbanization prospects: the 2014 revision highlights. United Nations, New York
- Valone TJ, Templeton JJ (2002) Public information for the assessment of quality: a widespread social phenomenon. *Philos Trans R Soc Lond B* 357(1427):1549–1155. <https://doi.org/10.1098/rstb.2002.1064>
- Viñuela J (2000) Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. *Behavioural ecology and Sociobiology* 48:333–343
- Wang Y, Bakker F, de Groot R, Wortche H, Leemans R (2015) Effects of urban trees on local outdoor microclimate: synthesizing field measurements by numerical modeling. *Urban Ecosystems* 18(4):1305–1331. <https://doi.org/10.1007/s11252-015-0447-7>
- Warren PS, Lepczyk CA (2012) Beyond the gradient: insights on new work in the avian ecology of urbanizing lands. In: Lepczyk CA, Warren PS (eds) *Urban bird ecology and conservation*. University of California Press, Berkeley, pp 1–6. <https://doi.org/10.1525/california/9780520273092.003.0001>
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York. <https://doi.org/10.1007/978-0-387-87458-6>

Principal Component 1: **Increasing access to Ritual subsidies**

NEST LOCATION

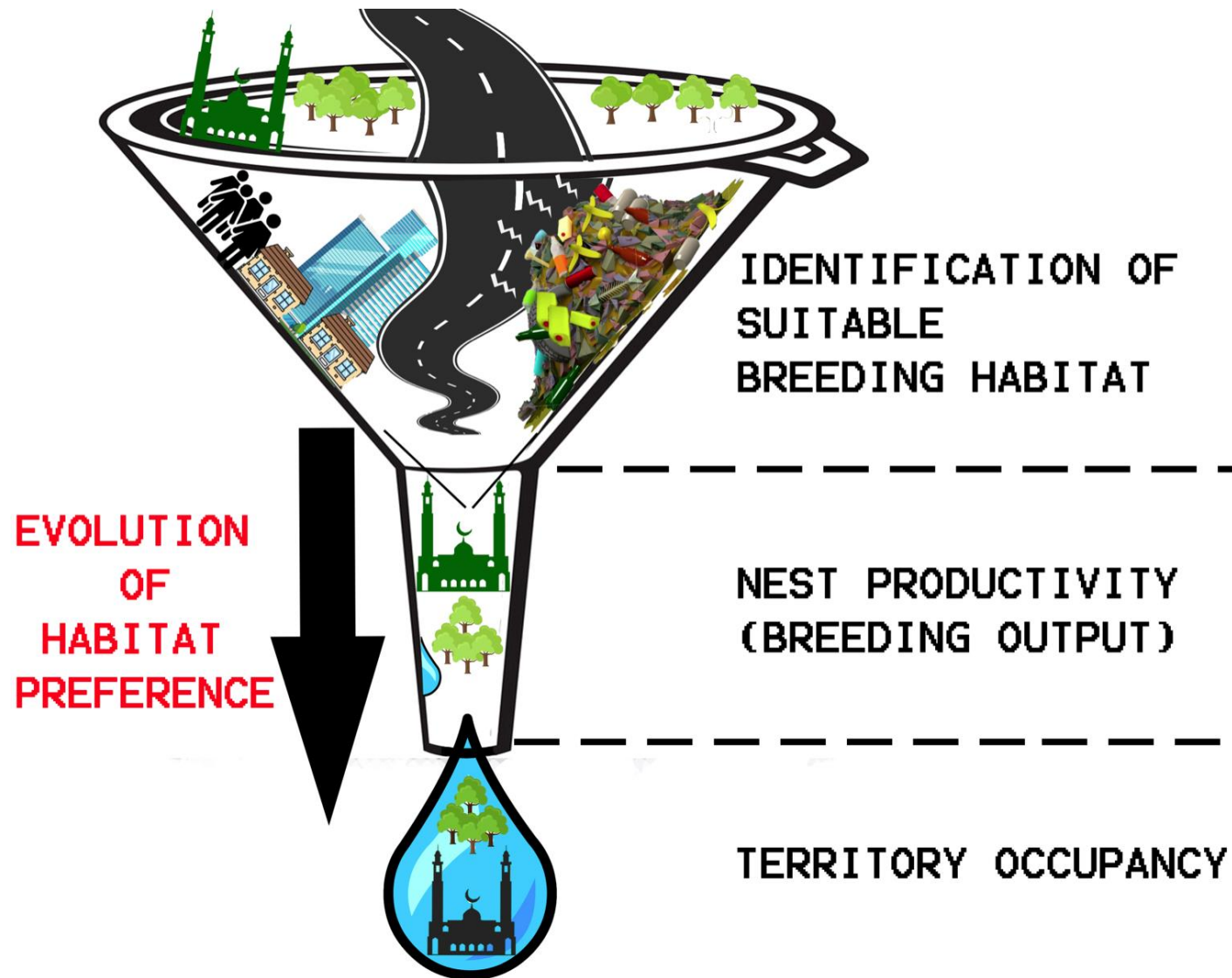


RANDOM LOCATION



(+) ve load of # people & (-) ve loading of distance to an old colony

A schematic depicting the Principal Component 1 extracted by using four independent variables: number of Muslims within a 2000 m radial area, and three successive distances to the Muslim pockets (colonies) from the point location (nest/random point). (Chapter 2,3,4 & 5).



A schematic depicting the mechanism of evolution of habitat selection by the breeding Black Kites in an urban habitat (Chapter 2 and 5). Note that the funnel and water droplet have been used to depict an analogy.

Online Resource 1

Table A1: Environmental variables measured at Black Kite nests and random locations in Delhi (India).

Variable	Description
<i>Nest-area scale:</i>	
Nest substrate	0 = tree; 1 = artificial structure (pylon, metal tower, electricity pole, building)
Nest tree species	Species of the nesting tree
DBH (cm) ^a	Diameter of the tree trunk at 1.4 m above the ground
Tree or pylon height (m)	Height of the nesting tree or artificial structure
Nest height (m)	Height of the nest above the ground
Tree arrangement	Categorical variable: 1 = isolated tree/pylon; 2 = line of trees (e.g. along an avenue); 3 = parkland (scattered trees with > 5-10 m of open ground between them, typically grassland in urban parks); 4 = woodlot
Woodlot Size (ha)	Size of the woodlot (only for locations classed as 4 above)
<i>Urban scale: landscape structure and composition</i>	
Index of buildings' density	Number of buildings crossed by a 500 m north-south and a 500 m east-west transect crossing each other on the nest/random location
Index of road density	Number of asphalted roads crossed by a 500 m north-south and a 500 m east-west transect crossing each other on the nest/random location
Urban cover	Percentage area covered by built-up structures (buildings, roads, parking lots, or any other impervious surface) within 500 m of the nest/random location
Green cover	Percentage area covered by shrub/tree vegetation within 500 m of the nest/random location
Open habitats	Percentage area free of built-up structures or arboreal vegetation within 500 m of the nest/random location (e.g. water, grassland, cultivated fields, rocky outcrops etc).
Habitat diversity	Shannon-Wiener index of habitat diversity based on the three land cover variables above

Distance to road (m)	Distance to the nearest asphalted road
Distance to water (m)	Distance to the nearest water body
Distance to illegal dump (m)	Distance to the nearest illegal dump (self-created by citizens, not recognized by any local municipality and often present only for a limited period of time)
Distance to landfill (m)	Distance to the nearest, large, authorized refuse dump
<i>Human scale: variables characterising human presence, practices and activities</i>	
Historical setting	Categorical variable: 0 = more recently built portion of the city (New Delhi); 1 = older, more historical portion of the city (Old Delhi) ^b
Hygiene score	Level of sanitation: 1 = clean areas; 2 = areas under poor waste management regimes ^c
Human density	Average number of people walking within 2m of a stationary observer during 5 min at 10 locations randomly plotted within 200 m of the nest/random location ^d
Muslim Density	Estimate of the local density of Muslim inhabitants (see details of calculations in Appendix B)
Access to Muslim subsidies	First component PC1 of a principal component analysis on Muslim density and the proximity to the three closest Muslim colonies

^a For locations on artificial structures, the DBH of the structure was estimated as the value predicted (given its height) by a regression of tree height on DBH (calculate on tree-sites only).

^b Old Delhi has a higher abundance of old buildings, a higher share of Muslim population and a higher concentration of slaughterhouses and meat selling shops than the more recently built portion of the city. Thus, it may represent a macro-portion of the city with higher availability of human subsidies (details in Online Resource 2).

^c Categorical variable with two levels: 1 = efficient waste disposal with very scarce or no organic refuse in the streets; 2 = abundant and widespread refuse in the streets throughout the area, either in small frequent piles, in illegal ephemeral dumps, or as individual items scattered a bit of everywhere through all streets (see also Appendix B).

^d Counts were only operated between 10:00-17:00 hrs and avoided during atypical, momentary peak periods of human traffic, such as exits from work or schools, in order to maintain consistency across sites (details in Online Resource 2)

Online Resource 1

Table A2: Mean (± 1 SE) estimates of variables measured at 100 Black Kite nests and at 100 randomly chosen locations in Delhi, India. Differences between the two samples were tested by means of t-tests, or χ^2 tests for categorical variables. Symbols: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Variable	Nest Sites	Random Locations
<i>Nest-area scale:</i>		
Nest substrate ^{a, b}	88.31 %	80.52 %
DBH (cm) ^b	75.47 $\pm$ 2.97	68.86 $\pm$ 2.43
Tree or pylon height (m)	14.86 $\pm$ 0.72	15.62 $\pm$ 0.52
Nest height (m) ^b	11.86 $\pm$ 0.63	12.06 $\pm$ 0.54
Woodlot size (ha) ***	17.47 $\pm$ 2.67	2.89 $\pm$ 1.78
<i>Urban scale:</i>		
Index of buildings' density ^b ***	18.85 $\pm$ 1.52	27.45 $\pm$ 1.75
Index of road density ^b ***	7.12 $\pm$ 5.33	5.33 $\pm$ 0.26
Urban cover ^b ***	0.38 $\pm$ 0.02	0.53 $\pm$ 0.02
Green cover ^b ***	0.28 $\pm$ 0.02	0.19 $\pm$ 0.01
Open habitats	0.33 $\pm$ 0.02	0.28 $\pm$ 0.02
Habitat diversity ^b ***	0.96 $\pm$ 0.02	0.85 $\pm$ 0.02
Distance to road ^b (m)	81.33 $\pm$ 9.72	79.91 $\pm$ 8.41
Distance to water ^b (m)	220.32 $\pm$ 30.39	275.29 $\pm$ 22.62
Distance to illegal dump ^b (m)**	717.08 $\pm$ 68.20	435.43 $\pm$ 46.82
Distance to landfill ^b (m)	6964.70 $\pm$ 318.42	7175.70 $\pm$ 355.44
<i>Human scale:</i>		
Historical setting ^c ***	71 %	38 %
Hygiene score ^{b, d} *	66.23 %	50.65 %
Human density ^b ***	12.96 $\pm$ 0.97	7.28 $\pm$ 0.65
Muslim Density **	32223 $\pm$ 2552.13	21296 $\pm$ 2231.5
Access to Muslim subsidies ^b **	0.25 $\pm$.09	-0.17 $\pm$ 0.1

^a Percent of nest / random locations on trees.

^b Variable that was fitted to the multivariate models of Table A3.

^c Percent of nest / random locations located in Old Delhi.

^d Percentage of locations with poor sanitation.

Online Resource 1

Table A3: Logistic regression (a) and linear mixed models (b, c) testing the effect of environmental and human variables on nest site selection (a), territory occupancy (b) and offspring production (c). Plot identity was added as a random factor to all models (see Methods).

Variable	B ± SE	Z-test	P- value
a. Dependent variable: nest-site selection ^{a,b}			
(N = 100 nests vs 100 random locations)			
Tree arrangement (tree line) ^c	0.26 ± 0.74	0.35	0.729
Tree arrangement (parkland) ^c	1.65 ± 0.69	2.41	0.015
Tree arrangement (woodland) ^c	2.94 ± 0.86	3.43	< 0.001
Index of road density	0.34 ± 0.11	3.10	0.002
Urban cover	-7.18 ± 2.06	-3.50	<0.001
Green cover	-1.00 ± 2.88	-0.34	0.731
Human density	0.17 ± 0.05	3.33	< 0.001
Hygiene score	2.38 ± 0.63	3.78	< 0.001
Access to Muslim subsidies	-0.33 ± 1.06	-0.31	0.758
Access to Muslim subsidies * Green cover	8.55 ± 2.87	2.98	0.003
Access to Muslim subsidies * Hygiene score	-2.02 ± 0.80	-2.53	0.011
Intercept	-3.24 ± 1.64	-	-
b. Dependent variable: occupancy ^d (N = 153 ^e)			
Tree arrangement (tree line) ^c	0.20 ± 0.28	0.72	0.471
Tree arrangement (parkland) ^c	0.52 ± 0.20	2.56	0.011
Tree arrangement (woodland) ^c	0.35 ± 0.22	1.59	0.111
Access to Muslim subsidies	0.14 ± 0.07	2.11	0.035
Intercept	0.43 ± 0.19	-	-
c. Dependent variable: fledglings produced in four years ^f (N = 153 ^e)			
Tree arrangement (tree line) ^c	0.09 ± 0.36	0.26	0.798
Tree arrangement (parkland) ^c	0.74 ± 0.25	2.95	0.003
Tree arrangement (woodland) ^c	0.23 ± 0.27	0.87	0.384
Access to Muslim subsidies	0.28 ± 0.08	3.51	< 0.001
Intercept	0.03 ± 0.23	-	-

^a Generalised linear mixed model with binomial errors and a logit link function. The model discriminated between 100 kite nests and 100 random locations.

^b Variables presented to the model: Nest substrate, DBH, Tree or pylon height, Nest height, Tree arrangement, Woodlot size, Index of building density, Index of road density, Urban cover, Green cover, Habitat diversity, Distance to road, Distance to water, Distance to illegal dump, Distance to landfill, Hygiene score, Human density, Access to Muslim subsidies, Access to Muslim

subsidies*Urban cover, Access to Muslim subsidies*Green cover, Access to Muslim subsidies*Hygiene score, Human density*Hygiene score (details of the rationale for fitting interactions can be found in the Methods). Variables of Table A1 not presented to the model to avoid collinearity: Open habitats, Historical setting.

^c Categorical variable with four levels: 1 = isolated tree/pylon, 2 = line of trees, 3 = parkland, 4 = woodlot.

^d Generalised linear mixed model with Poisson errors and a logit link function. The dependent variable is the number of years that a territory was occupied, which ranged from 1 to 4.

^e One territory (of the overall sample of 154 territories used for building the nesting habitat selection model) could not be sampled after the first year for logistic reasons (inability to access a private property). Thus, the occupancy and breeding success models were based on a sample of 153 territories, each sampled in all the four years of investigation.

^f Generalised linear mixed model with Poisson errors and a logit link function. The dependent variable is the number of young raised to fledging age in four years, which ranged from 0 to 9.

Online Resource 2

Access to human subsidies by Delhi kites: rationale and estimation

In Delhi, kites obtain their main food (meat waste from humans, Kumar et al., 2014) from three major sources: (1) dump (garbage landfill) sites, although these are mainly used by non-breeding kites; (2) roads, especially those with a high density of commercial activities and families, who often dispose their personal waste by leaving it directly in the streets, which may in turn attract potential complementary live prey for kites, such as rodents or pigeons (Kumar et al., 2014, authors' unpublished nest camera-trapping data); (3) direct and indirect effects of religio-cultural practices, such as the higher abundance of meat selling shops and the ritualized-feeding by people who follow Islamic faith in Muslim colonies and in the older establishments of the city (Old Delhi). Thus, because direct, quantitative measurements of such capillary-distributed subsidies would be impossible over such large areas, we considered that proximity to dump sites, local human density in the streets, and religious zoning could be potential surrogates of kite food availability. Therefore, for each nest or random location, we calculated the following variables.

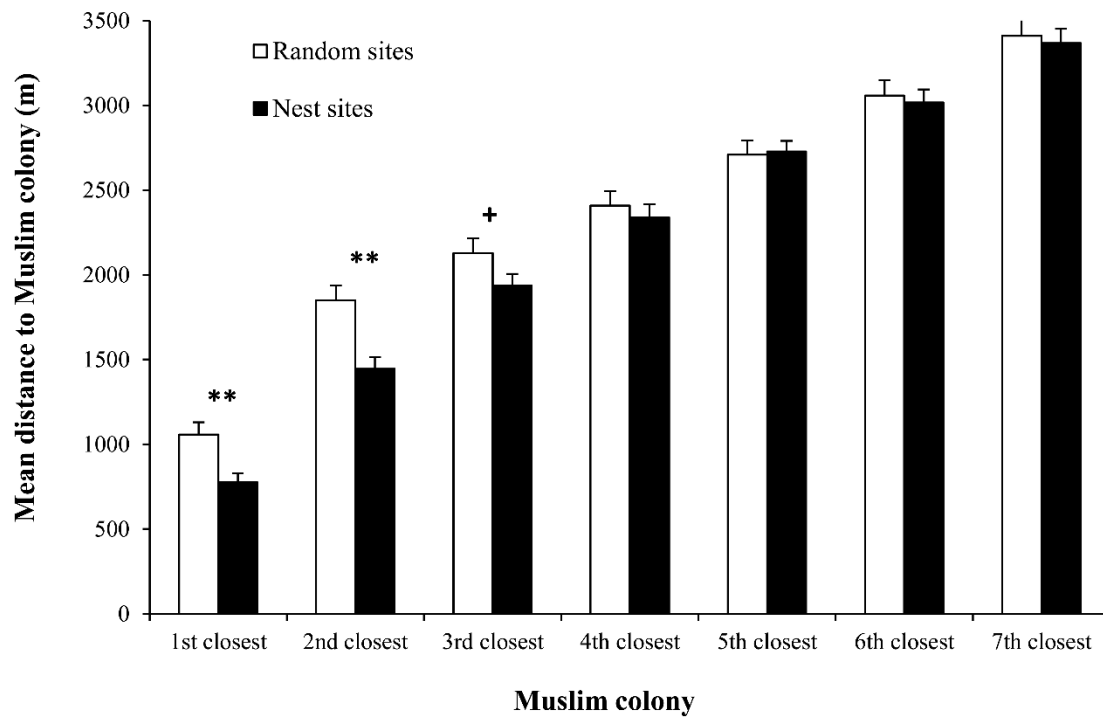
(1) First, we measured the distance to the nearest legal or illegal refuse dump site. Such dumps were easily located during our fieldwork on the basis of frequent observation of unauthorized disposal of garbage at certain sites of each plot, where piles of refuse accumulated in evident manners. (2) Second, human traffic and density in the streets was estimated by counting for five minutes the number of people who passed by a stationary observer at 5-10 randomly plotted locations (depending on local conditions, e.g. less points in rural plots with few roads) along the roads within a circle of 200 m centred on each nest or random location. To standardize them as much as possible in relation to human activities, these counts were operated exclusively during working days and between 1000 - 1700 hrs, and halted during unusual events that could have

biased the estimates (e.g. sudden exit from work or local schools). (3) Third, we interviewed 10 random people in the streets around the nests and random locations about the routine removal of garbage from the local dumps, and integrated it with our own observations of local conditions to create a hygiene index, which classed sites as relatively clean with little litter in the streets and constantly low refuse availability for kites, or as more dirty, with constant presence of large garbage piles in the streets, or in close proximity to stable rubbish dumps (Online Resource 1).

(4) Fourth, in the absence of fine-scale data on human population density by religion, we estimated the number of inhabitants of Muslim faith within a 2 km circle centred on each nest or random location in the following manner. First, we extracted the number of Muslim inhabitants for each sub-district of the city, using the 2011 census data (<http://censusindia.gov.in/2011census>). Second, we digitized the areal extent of Muslim colonies in each sub-district using Google Earth Pro Imagery and our own ground visits to such colonies. Third, we divided the Muslim population of each sub-district by the area of Muslim colonies within each sub-district to obtain a gross estimate of local Muslim density/unit area, under the assumption that the majority of the Muslim population was concentrated at such “closed” colonies (as supported by well-known and widespread religious ghettoization in India: see Gupta 1998 and Kirmani 2013 for details). Fourth, we multiplied such local density by the actual area of Muslim colonies included in each 2 km-circle, so as to re-adapt the sub-district level Muslim density to the circle around each nest or random location. (5) Finally, we classed locations as placed in the old section of the city (Old Delhi) or within the more recently built up areas (New Delhi). These two categories represented macro-areas under different forms of urbanization history and intensity, configuration, and hygiene, Old Delhi including a large share of Muslim colonies with poor sanitation as well as high concentrations of meat shops.

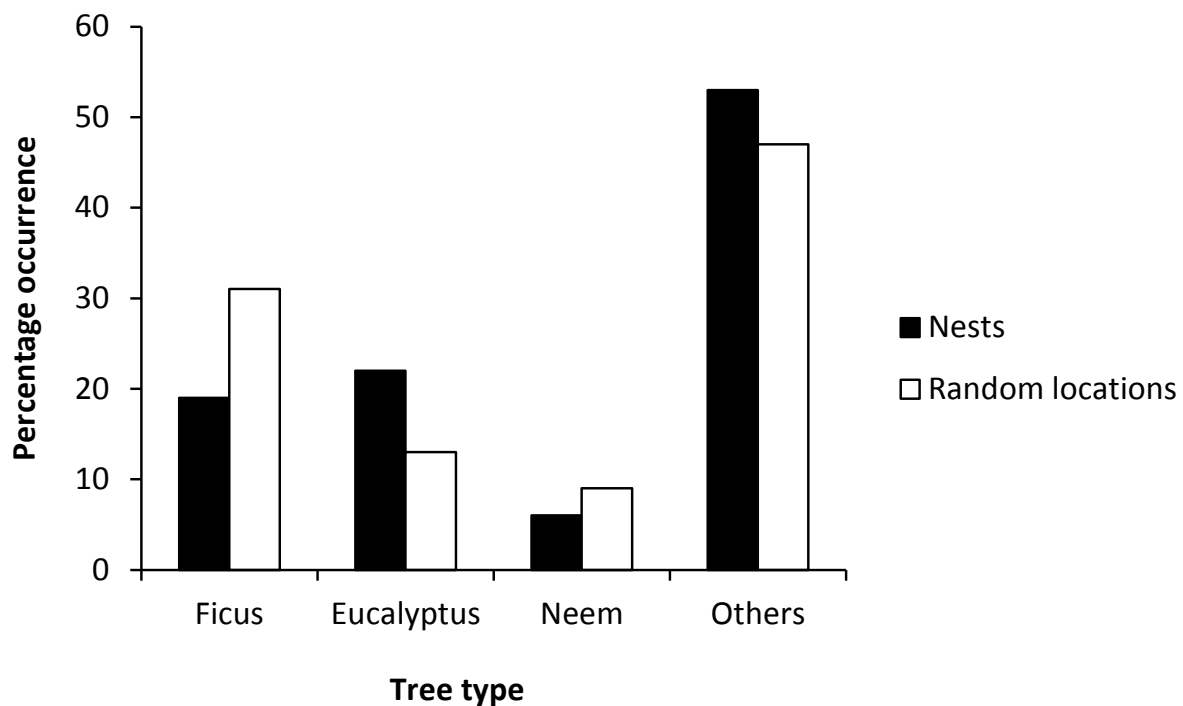
Online Resource 3

Mean distance to Muslim colonies for 100 Black Kite nests (black bars) and 100 random locations (white bars) in Delhi (India). The difference between kite nests and random locations was significant for the first and second closest Muslim colony, and marginally significant for the third closest Muslim colony, suggesting over-selection of sites close to multiple sources of ritual subsidies. Symbols: ** $P < 0.01$; + $P < 0.1$. Error bars represent 1 SE.



Online Resource 4

Proportional incidence of tree species among kite nests and random locations in Delhi. There was no significant over-selection or avoidance by kites of main tree species type ($\chi^2 = 6.15$, $P = 0.104$). The category “Other tree species” incorporated all tree species which occurred less than 5 times among kite nests or random locations and included the following species: Honey mesquite *Prosopis juliflora* (N = 12 for nests and 0 for random locations), Jamun *Syzygium cumini* (10, 1), Semal *Bombax ceiba* (4, 8), Devil’s tree *Alstonia scholaris* (3, 4), Indian rosewood *Dalbergia sissoo* (3, 3), Gulmohar *Delonix regia* (2, 0), Siris *Albizia lebbek* (0, 2), Mango *mangifera indica* (1,1), Cottonwood *Populus gamblei* (1, 1), Dinner Plate tree *Pterospermum acerifolium* (1,0), Monkeypod *Pithecellobium dulce* (0, 1), Unidentified (2, 3).



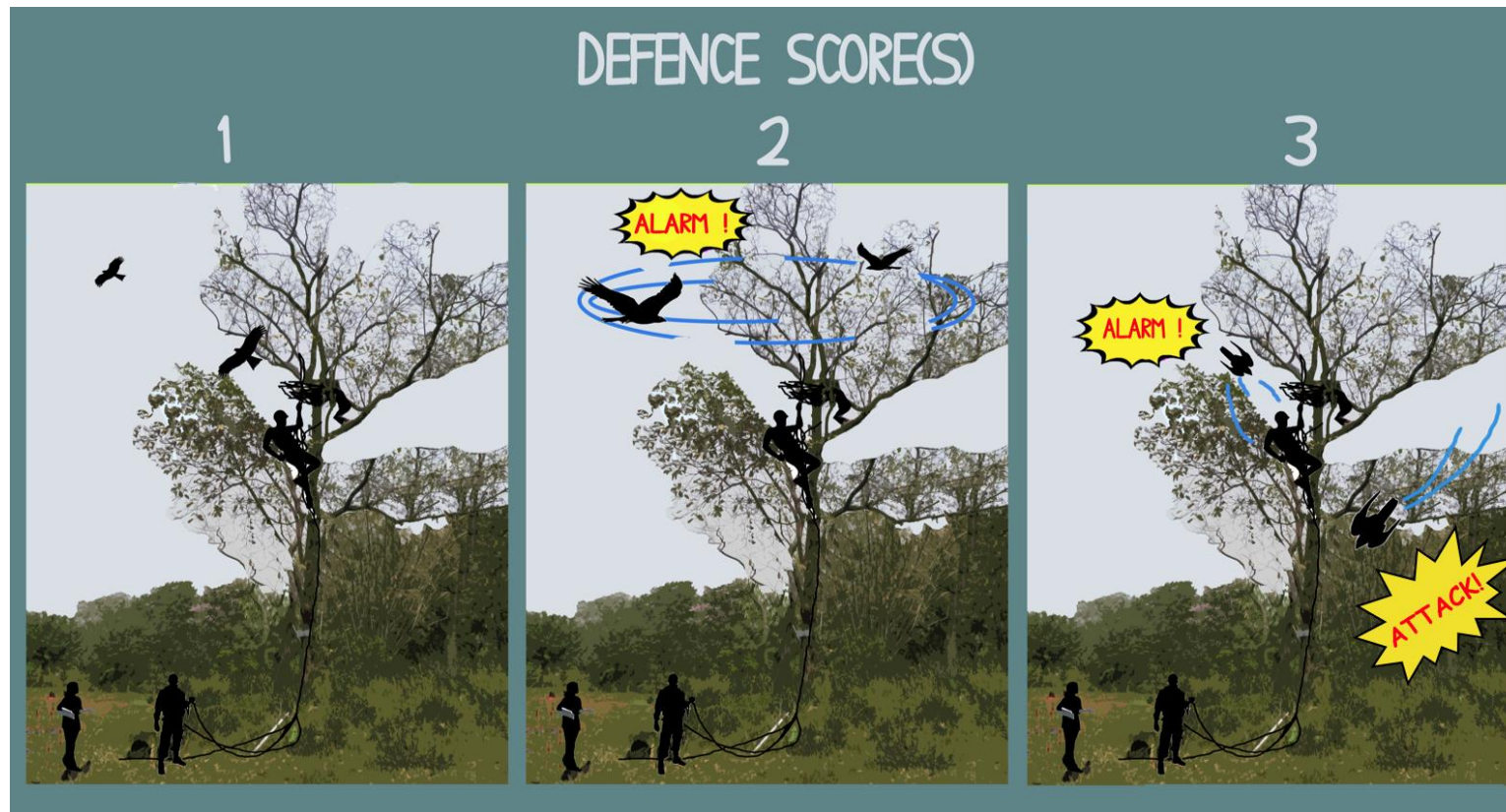
Offspring defense by an urban raptor responds to human subsidies and ritual animal-feeding practices

Nishant Kumar, Qamar Qureshi, Yadvendradev V. Jhala, Andrew G. Gosler & Fabrizio Sergio

*Originally published on October 29, 2018; Volume 13(10), **PLoS ONE**.*

Abstract

There is a growing interest in the behavioural and life history mechanisms that allow animal species to cope with rapidly expanding urban habitats, which impose frequent proximity to humans. A particular case of behavioral bottleneck (i.e. conflicting interests) faced by animals in urban environments is how they will modulate the defence of their offspring against the potential danger represented by humans, an aspect that has received scarce research attention. We examined the nest defense against humans by a dense breeding population of a raptor, the Black Kite *Milvus migrans*, within the megacity of Delhi (India). Here, kites live on a diet dominated by human waste and meat offered through religiously motivated bird feeding practices. Nest defense levels increased with the number of offspring, and with the progression of the breeding season. Defense also intensified close to ritual-feeding areas and with increasing human waste in the streets, suggesting synergistic effects of food availability, parental investment, personality-boldness and habituation to humans, with consequent attenuation of fear. Thus, the behavioural response to a perceived threat reflected the spatial mosaic of activity of humans in the city streets, their cultural practices of ritual-feeding, and their waste-management. For synurbic species, at the higher-end spectrum of adaptation to an urban life, human cultural practices and attitudes may well be the most defining dimensions of their urban niche. Our results suggest that, after initial urban colonization, animals may continue to adapt to the typically complex, heterogeneous environments of cities through fine-grained behavioural adjustments to human practices and activities.



Nest Content?

Period of nesting?

Habituation?

Habitation?

A schematic depicting the three ordinal increasing levels of offspring defence by the resident Black Kite race (Chapter 3 & 4).

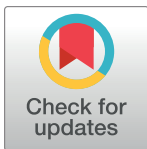
RESEARCH ARTICLE

Offspring defense by an urban raptor responds to human subsidies and ritual animal-feeding practices

Nishant Kumar^{1,2*}, Qamar Qureshi², Yadvendradev V. Jhala², Andrew G. Gosler^{1,3}, Fabrizio Sergio⁴

1 Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, Oxford, United Kingdom, **2** Wildlife Institute of India, Chandrabani, Dehradun, Uttarakhand, India, **3** Institute of Human Sciences, School of Anthropology and Museum Ethnography, Oxford, United Kingdom, **4** Department of Conservation Biology, Estacion Biologica de Doñana—CSIC, C/ Americo Vespucio 26, Sevilla, Spain

* nishant.kumar@zoo.ox.ac.uk, nishant@wii.gov.in



Abstract

There is a growing interest in the behavioural and life history mechanisms that allow animal species to cope with rapidly expanding urban habitats, which impose frequent proximity to humans. A particular case of behavioral bottleneck (i.e. conflicting interests) faced by animals in urban environments is how they will modulate the defence of their offspring against the potential danger represented by humans, an aspect that has received scarce research attention. We examined the nest defense against humans by a dense breeding population of a raptor, the Black Kite *Milvus migrans*, within the megacity of Delhi (India). Here, kites live on a diet dominated by human waste and meat offered through religiously motivated bird feeding practices. Nest defense levels increased with the number of offspring, and with the progression of the breeding season. Defense also intensified close to ritual-feeding areas and with increasing human waste in the streets, suggesting synergistic effects of food availability, parental investment, personality-boldness and habituation to humans, with consequent attenuation of fear. Thus, the behavioural response to a perceived threat reflected the spatial mosaic of activity of humans in the city streets, their cultural practices of ritual-feeding, and their waste-management. For synurbic species, at the higher-end spectrum of adaptation to an urban life, human cultural practices and attitudes may well be the most defining dimensions of their urban niche. Our results suggest that, after initial urban colonization, animals may continue to adapt to the typically complex, heterogeneous environments of cities through fine-grained behavioural adjustments to human practices and activities.

OPEN ACCESS

Citation: 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(10): e0204549. <https://doi.org/10.1371/journal.pone.0204549>

Editor: Antoni Margalida, University of Lleida, SPAIN

Received: April 29, 2018

Accepted: August 15, 2018

Published: October 29, 2018

Copyright: © 2018 Kumar et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are available on the Oxford Research Archive: <https://doi.org/10.5287/bodleian:KZPgrPVzg> (DOI: [10.5287/bodleian:KZPgrPVzg](https://doi.org/10.5287/bodleian:KZPgrPVzg)).

Funding: The project was funded through multiple grants (2013–2016) by the Raptor Research and Conservation Foundation (Mumbai) <http://raptors.net.in/> to NK and by the Govt. of India, Ministry of Environment, Forest and Climate Change to YVJ, and NK). N. Kumar's D. Phil (2014–18) at the University of Oxford was funded by the Felix

Introduction

Rapid, worldwide urbanization is raising interest in urban ecology and in the ways animals adapt to novel and burgeoning urban environments [1]. In particular, behavioural mechanisms that mediate such adaptation remain an under-researched topic [2, 3], with current

Scholarship Trust and Somerville College (<https://www.somerville.ox.ac.uk>; Discretionary Grant 2017). Funding for travelling and fieldwork by F. Sergio was afforded by Project CGL2015- 69445-P of the Spanish Ministry of Economy and Competitiveness.

Competing interests: The authors have declared that no competing interests exist.

knowledge mostly limited to a handful of species that have only recently colonized or are in the process of capitalizing on urban environments e.g. [2, 4, 5]. Furthermore, these species have typically been studied in biogeographic regions with a long history of wildlife persecution by humans, whose proximity is frequently seen as a potential obstacle for urban colonization e.g. [6, 7]. For example, many studies have focused on flight initiation distances (FID) to explore how behavioural characteristics or personality features may allow certain individuals to better cope with proximity to humans in highly anthropogenic environments [8–12].

A different scenario may be represented by those ‘synurbic’ species [13] that have lived within human settlements for centuries. These species often show limited fear of humans and sometimes even directly exploit them, as in the case of many populations dependent on carrion or garbage in traditional human societies which, often because of the ecosystem services they provide, do not persecute them e.g. [14]. Information on the behavioural responses to humans by these urban specialists would complete our current picture of adaptation to a rapidly urbanising world and offer insights into the range of behavioural strategies potentially employed by urban wildlife to cope with a constant high proximity to humans [15, 16].

One particularly interesting case of behavioural bottleneck (i.e. conflicting interests) faced by animals in urban environments is how to modulate their defence of young in a fixed nest or den against the potential danger presented by humans. Such modulation is especially relevant for large vertebrates armed with potentially dangerous weaponry and thus theoretically capable to drive humans away. This scenario is more complex than the one examined in studies of flight initiation distance, because the fitness investment at stake (the offspring) is not mobile and cannot be fully controlled by the animal (e.g. by fleeing). Thus, it may be particularly informative of the extent to which urban animals perceive humans as a threat, how much risk they are willing to take to defend their parental investment, and how this may vary along a range of urban configurations and human attitudes towards wildlife. To our knowledge, few studies have examined such aspects and most of them have focused essentially on the comparison of behavioural traits between urban and rural individuals (review in [2, 7]). While this comparison renders important information on trait expression associated with the colonization of urban environments, it assumes that all individuals that colonized a city adopted the same behavioural strategies [16]. However, urban environments are often highly heterogeneous mosaics with marked variation in physical structure or human density [17, 18], to which animals are likely to respond, potentially selecting for a more complex array of behavioural strategies in urban animals than has thus far been recognized.

To explore these aspects, here we examine patterns of nest defense against humans by a synurbic raptor, the Black Kite *Milvus migrans*, which exploits humans for food in a megacity (Delhi, India) that incorporates a wide range of urban conditions, human densities and ritualized animal-feeding practices. The Black Kite (hereafter kite) is a medium-sized opportunistic raptor, widely distributed throughout Eurasia, Africa and Australia, and considered the most successful raptor in the world. In India, the native, resident subspecies *M. m. govinda* is synurbic (sensu [13]), occurring almost exclusively in close association with humans in towns and cities [19]. In Delhi, kites breed on both trees and artificial structures (pylons, towers), sometimes forming loose colonies and locally reaching extremely high densities, thanks to the exploitation of human food ‘subsidies’ facilitated by inefficient refuse disposal and by religious kite-feeding practices [20, 21]; (see Study area below). In particular, the relationship between kites and humans in Delhi is dual: on one hand, kites depend on humans for food and thus over-select breeding sectors in the city close to ritual-feeding sites, and with a high density of humans and of their garbage in the streets [20]. On the other hand, people sometimes rob or destroy kite nests to collect nestlings for the illegal bird trade, or to remove dangerous nest materials from electricity pylons, telephone towers or light poles during maintenance

operations [22]. Thus, humans approaching a nest can be perceived by kites as a potential threat to their offspring, soliciting a defense response.

We feel that this represents a particularly interesting case study because: (1) Delhi kites directly exploit humans for food, by accessing their waste or by grabbing meat offered to them by people through religious, ritual feeding practices. Thus, they frequently come into close contact with humans, which may affect their perception and fear of humans. (2) These offerings and garbage disposal practices vary dramatically through the city (see Study area below), implying that different kites may experience and perceive people in different ways through the urban mosaic. (3) As medium-sized raptors armed with sharp talons and high aerial agility, kites are potentially well capable to inflict injury on people and drive them away from their nest-area. However, (4) much of the mortality experienced by kites is still of anthropogenic origin [22], implying a delicate trade-off between the need to come close to humans for feeding but avoid them or repel them in the appropriate context to ensure their own or their offspring safety. Given all the above, when faced with people approaching their nest, kites will need to take a quick defense-tactic decision, which may reflect these conflicting pressures. Furthermore, the balance of these pressures may change through the complex mosaic offered by this megacity of 16 million people. In particular, because ready access to dense Muslim colonies rich in ritual-subsidies is considered a key resource in this population (see [20, 21] and Study area below), we hypothesized that it could alter the profitability for kites of hygiene levels, green cover or built-up cover, ultimately affecting the defense-value of the offspring.

Materials and methods

This research is part of a larger and long-term study on the demography of Black Kites in Delhi and has received bioethical approval by the Training, Research, and Academic Council (TRAC) of the Wildlife Institute of India, Dehradun. The project took all precautions to ensure researcher and animal safety. The study did not involve human participants other than the research team.

Study area

Delhi is a megacity of more than 16 million inhabitants, currently covering an area of 1500 km² and in constant, rapid expansion [23]. It is polycentric and heterogeneous, with a multitude of juxtaposed urban configurations, which make it difficult to establish a linear urban-rural gradient. Two aspects of Delhi are important in determining the food availability and habitat quality for kites [20]. First, large portions of the city are characterized by poor solid waste management, which affords food to kites in the form of carrion or refuse, and its associated prey-fauna (e.g. rodents, pigeons etc.). Secondly, many people (primarily in Muslim settlements) 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. These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries [24, 25]. Thus, waste management issues common to all communities, and cultural rituals which are more specific to some, generate spatial heterogeneity in the potential food availability for kites [20].

Field procedures

We systematically surveyed kite nests during 2013–2016 at 24 plots of 1 km², which were randomly stratified within Delhi (1500 km²) so as to cover all its possible urban settings, from semi-natural to extremely built-up sites (details in [21]). This resulted in a sample of 101 nests, each from a different territory, used at least once for breeding between 2013 and 2016. Nests

were checked every 7–10 days until the chicks were at least 45 days old, in order to estimate the number of young raised to fledging (chicks fledge when about 48 days old) (see [21] for further details of nest checks and surveys). During each nest check, we assessed the intensity of offspring defense by the parents against our own human intrusion as follows. During each visit, a team consisting of a tree-climber (always the same for each nest) and one or two accompanying observers positioned themselves at a point from where the kite nest was in clear sight. The point was chosen so as to be clearly visible to the parent kite perched in the nest area. The team then walked slowly towards the nest. Once under the nest, we observed the behaviour of the adults for 20 minutes while the tree-climber reached the nest and checked its content. We classified the intensity of defense according to the following ordinal score: (score 0) the kite remains perched at a distance (> 20 m) or flies far away, either silently or after alarm-calling a few times; (score 1) it flies directly above the field-team in an excited manner while calling repeatedly, or perches close-by (within 20 m) and alarms continuously, or perches within a few metres of the climber (within the same nesting tree); and (score 2) it repeatedly dive-bombs at the climber and ground-team, it may even stoop among tree-branches or electricity wires, or perch a few metres from a team-member and then stoop again, sometimes hitting or scratching with open talons, while continuously alarm-calling. Thus, progressively higher scores were associated with higher costs and risks for the defending kite, including (a) increases in energy costly activities, such as alarm-calling or flapping flight, and (b) increases in potential risks, such as injuries while manoeuvring through the canopy or overhead electric wires. Throughout, the defense score refers to the maximum intensity of defense shown by either of the partners of each pair. This was justified by the fact that: (1) kites are monomorphic, making it impossible to distinguish males from females; and (2) no difference in defense levels was noticed between the two partners of a pair (if one attacked, the other also attacked, while if one remained quietly perched, the other did the same). All defense ratings were carried out between 08:00 and 18:00 hrs (local time) avoiding unusual weather conditions (e.g. rain, or excessive heat).

Predictors of offspring defense

To investigate how kite defense varied across the Delhi mosaic of urban structure, human densities and practices, we measured a series of environmental, urban and human variables previously found to be important components of habitat quality and food availability in this population [20]. These variables are detailed in Table 1 and were devised so as to characterise: (1) the timing, context and characteristics of the defense trial (e.g. number of people in the visiting team, number of previous visits to a target nest); (2) the breeding stage, social setting (intraspecific spacing) and content of the nest during the trial (e.g. number of offspring to be defended); (3) the physical features of the nest and its immediate surroundings (e.g. its location within a hedge, park or continuous woodland); (4) the urban landscape structure around the nest (e.g. local road density or extent of impervious surfaces in the surroundings); and (5) direct and indirect estimates of human activities and practices (e.g. access to dense Muslim colonies for reasons stated above, efficiency of waste management, or human density). Further details of the recorded variables and their ecological rationale are given in Table 1 and in [20].

In particular, a key variable in our previous analyses on the predictors of kite site selection, occupancy and breeding performance was the ease of access to dense Muslim colonies, which provide abundant food supplies in the form of ritual subsidies [20]. More specifically, we previously showed that Delhi kites over-selected for breeding sites closer than available to the 1st, 2nd and, possibly, 3rd nearest Muslim colony (see [20] for details). Thus, to provide a comprehensive measure that integrated the proximity to the three nearest Muslim colonies with their

Table 1. Variables measured during nest defense trials conducted at Black kite nests within the city of Delhi (India).

Variable	Description, rationale for use and predicted effect
Julian date	Julian date of nest inspection. Earlier laying raptors are often older or higher quality individuals with higher parental investments and were thus expected to be more aggressive [52].
Breeding stage	The breeding cycle was divided into five main stages: (1) pre-incubation; (2) incubation (3) nestlings younger than 15 days; (4) nestlings of 15–30 days; (5) pre-fledging: 30–48 days old nestlings; (6) post-fledging. We expected defense to vary by stage because avian nest defense often varies through the breeding season in conjunction with the growing survival probabilities of the offspring e.g. [33–35].
Previous visits	Number of previous nest checks by the research team. This variable was fitted to control for potential habituation or reinforcement of aggressiveness by repeated sampling of the same pair [53].
Team size	Number of people in the research team (2 or 3). This was fitted to examine the impact of the number of intruders on defense, if any.
Number of onlookers	Number of people (not belonging to the field-team) within 20 m of the nest during the defense trial. This was fitted to examine the impact of the number of onlookers on defense, if any.
Number of offspring	Number of eggs or chicks in the nest at the time of the defense trial. We expected higher aggression by pairs with larger parental investments, as found in some previous studies e.g. [33–35].
NND5 (m)	Mean distance to the five closest kite neighbors. This variable focused on the impact of local, spatial arrangement on defense intensity. We expected higher defense under more crowded conditions (i.e. at higher quality, more attractive sites, which may entail higher parental investments).
Territories within 200 m	Number of territories occupied within 200 m of the target nest. This variable focused on the impact of local density on defense intensity. We expected higher defense levels at higher local densities (i.e. at higher quality, more attractive sites, which may entail higher parental investments).
Colony size	Number of nests within the kite colony. We expected larger colonies to be more attractive to individuals of a semi-social species, or to be associated with higher vigilance and larger food supplies, leading to a higher motivation for defense.
Tree arrangement	Categorical variable: 1 = isolated tree/pylon; 2 = line of trees (e.g. along an avenue); 3 = parkland (scattered trees with > 5–10 m of open ground between them, typically grassland in urban parks); 4 = woodlot. These habitat configurations are known to be differentially attractive to Delhi kites [20] and were fitted in order to investigate links between habitat quality, urban landscape configuration and defense intensity.
Balcony	Categorical variable: 0 = absence, 1 = presence of a balcony within 20 m of the nest. We predicted that pairs in such close and constant contact with humans could show higher aggressiveness through habituation and loss of fear.
Index of road density	Number of asphalted roads crossed by a 500 m north-south and a 500 m east-west transect crossing each other on the nest. Delhi kites over-select areas with more extensive road networks, which are one of their main foraging habitats [20]. Thus, we expected defense-levels to increase with road density.
Urban cover	Percentage area covered by built-up structures (buildings, roads, parking lots, or any other impervious surface) within 500 m of the nest. Urban and tree cover were fitted to investigate links between offspring defense and urban landscape configurations. Urban cover was also fitted as a quadratic effect to test the “intermediate disturbance hypothesis” commonly proposed in the urban ecology literature [54], by which the favourability of urban ecosystems to wildlife peaks at intermediate levels of the urbanization gradient.
Green cover	Percentage area covered by shrub/tree vegetation within 500 m of the nest. Urban and tree cover were fitted to investigate links between offspring defense and urban landscape configurations.
Hygiene score	Level of sanitation: 1 = clean areas; 2 = areas under poor waste management regimes ^a . The level of street sanitation is an important component of habitat quality for this population [20]. We expected higher aggression at sites with lower sanitation because of frequent exposure to humans and because larger food supplies may imply larger broods and thus higher parental investments.

(Continued)

Table 1. (Continued)

Variable	Description, rationale for use and predicted effect
Human density	Average number of people walking within 2m of a stationary observer during 5 min at 10 locations randomly plotted within 200 m of the nest ^b . Delhi kites over-select sites with intense human activity in the streets, leading to more food in the form of human refuse [20]. We expected defense-levels to increase with human density in the streets because of frequent exposure to humans and because larger food supplies may imply larger broods and thus higher parental investments.
Access to Muslim subsidies	First component (PC1) of a principal component analysis on Muslim density and on the proximity to the three closest Muslim colonies (see Methods). Muslim subsidies are one of the main food resources for Delhi kites [20, 21] and ready access to them was predicted to boost offspring-defense because of frequent exposure to humans and because larger food supplies may imply larger broods and thus higher parental investments.

^a Categorical variable with two levels: 1 = efficient waste disposal with very scarce or no organic refuse in the streets; 2 = abundant and widespread refuse in the streets throughout the area, either in small frequent piles, in illegal ephemeral dumps, or as individual items scattered a bit of everywhere through all streets [20].

^b Counts were only operated between 10:00–17:00 hrs and avoided during atypical, momentary peak periods of human traffic, such as exits from work or schools, in order to maintain consistency across sites [20].

<https://doi.org/10.1371/journal.pone.0204549.t001>

human population density (under the assumption that higher rates of refuse and ritualized-feeding should occur in more densely-populated Muslim colonies), we extracted the first component of a PCA [26] run on these four aforementioned variables. Its PC1 (hereafter “access to Muslim subsidies”) explained 65% of the variance and had a high positive loading on Muslim population density and high negative loadings on the distance to the 1st, 2nd and 3rd closest Muslim colonies. Thus, it provided an increasing index of access to abundant “Muslim subsidies”.

Statistical analysis

We employed a linear mixed effect ordinal regression (cumulative-link mixed effect model), [27, 28] through package “ordinal” [29] to examine the effect of environmental, urban and human variables on the ordinal score of offspring defense. The ordinal regression was run on 657 defence trials conducted at 101 unique nesting territories. Because territories were sampled repeatedly, and because territories within the same plot were closer and thus potentially more similar than territories sampled in different plots, we fitted as a random effect territory identity nested within plot identity and year, so as to control for pseudoreplication and spatial autocorrelation [30]. To reduce collinearity and the number of variables presented to the logistic regression, we considered pairs of strongly inter-correlated variables ($r > 0.60$) as estimates of a single underlying factor, and only retained for analysis the one estimated to be more biologically important for the study organism.

To explore further the potential link between defense intensity and subsequent breeding benefits, we related the eventual number of fledged young to the intensity of defense during incubation (i.e. about two months before fledging) by means of a linear mixed model, again with territory identity nested within plot identity and year as a random term.

All multivariate models were built through a backward stepwise procedure following Zuur et al. [30]: all explanatory variables were fitted to a maximal model, extracted one at a time from the maximal model, 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 [30]. To avoid over-parameterization, we ensured never to fit more than $N/3$ variables to each maximal model, where N is the sample size of the

analysed dataset [31]. Interactions were fitted only when we had a priori hypotheses about their potential effect, based on our field observations and knowledge of the population. To explore the possibility of curvilinear relationships, we fitted continuous variables as linear and also as quadratic terms. Explanatory variables were fitted as standardized Z-scores because of their different measurement units and in order to better evaluate their relative importance [32]. Model assumptions were checked by investigating QQ plots, histograms of residuals, and plots of standardized and normalized residuals against fitted values and against explanatory variables [30, 31]. All mixed models were implemented in R.3.4.3 [33], all tests are two-tailed, statistical significance was set at < 0.05 , and all means are given ± 1 SE.

Results

Several variables entered the mixed model ordinal regression (Table 2). First, defense intensity increased progressively along the breeding cycle and then declined in its final stages, especially after the young fledged from the nest (Fig 1A). Second, defense levels increased with the number of offspring in the nest (Fig 1B). Third, the interaction of Access to Muslim subsidies and Hygiene score was also significant (Table 2 and Fig 1C): under conditions of poor sanitation,

Table 2. Cumulative-link mixed effect ordinal regression (a) testing the effect of environmental, urban and human variables on the ordinal intensity of offspring defense; and (b) linear mixed effect model testing the effect of intensity of offspring defense in incubation on eventual fledgling production.

Variable	$\beta \pm \text{SE}$	Z-test	P-value
a. Dependent variable: Intensity of defense (N = 657) ^{a,b}			
Breeding Stage (incubation)	1.11 ± 0.8	1.39	0.164
Breeding Stage (small nestling)	3.11 ± 0.82	3.81	< 0.001
Breeding Stage (large nestling)	3.83 ± 0.8	4.78	< 0.0001
Breeding Stage (pre-fledging)	2.34 ± 0.76	3.07	0.002
Breeding Stage (post-fledging)	0.71 ± 0.97	0.73	0.463
Offspring number	1.61 ± 0.33	4.81	< 0.0001
Access to Muslim subsidies	-6.23 ± 2.01	-3.1	0.001
Hygiene score	3.25 ± 1.01	3.24	0.001
Access to Muslim subsidies * Hygiene score	4.5 ± 2.02	2.22	0.026
Green cover	-1.65 ± 0.68	-2.4	0.016
Urban cover	-3.69 ± 1.62	-2.28	0.022
Urban cover ²	3.20 ± 1.67	1.9	0.057
b. Dependent variable: fledglings produced ^c (N = 103)			
Intensity of defense (during incubation)	0.28 ± 0.12	2.27	0.023
Intercept	-0.36 ± 0.17	-	-

^a Cumulative link mixed model with a logit link function, based on N = 657 defense trials from 101 independent territories. The dependent variable is the ordinal score of offspring defense intensity. Territory-identity nested within plot-identity and year was fitted as a random factor.

^b Variables presented to the model: Julian date, Team size, Number of onlookers, Previous visits, Breeding Stage, Offspring number, NND5, Territories within 200 m, Tree arrangement, Balcony, Index of road density, Urban cover, Green cover, Hygiene score, Human density, Access to Muslim subsidies, Access to Muslim subsidies*Hygiene score, Access to Muslim subsidies*Urban cover, Access to Muslim subsidies*Green cover (the rationale for fitting interactions can be found in the Methods).

^c Generalised linear mixed model with Poisson errors and a logit link function, based on N = 103 defense trials from 60 independent territories sampled during incubation. The dependent variable is the number of young raised to fledging stage. Territory-identity nested within plot-identity and year was fitted as a random factor.

<https://doi.org/10.1371/journal.pone.0204549.t002>

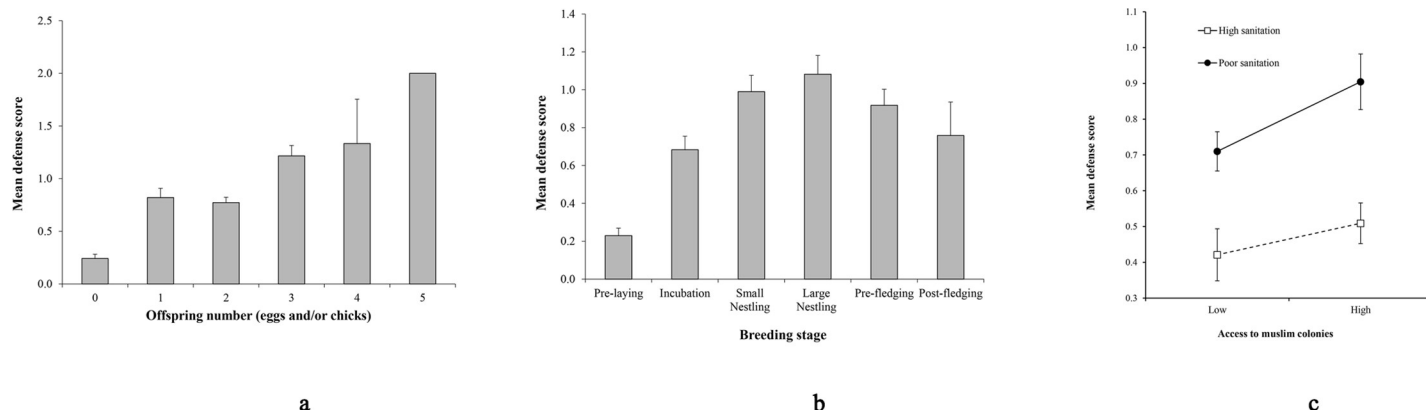


Fig 1. The intensity of offspring defense by kites in Delhi (India) varied with: panel (a) the stage of the breeding cycle; panel (b) the number of offspring (eggs and/or chicks) in the nest at the time of the defense trial; and panel (c) the interaction between access to Muslim subsidies and the amount of human waste in the streets (the black circles and the solid line indicate breeding sites with poor street sanitation, while the white quadrats and dotted line portray cleaner sites with less refuse in the streets). In panel c, Access to Muslim subsidies is shown above and below the median value ("high" and "low", respectively) for clarity of presentation. Error bars represent ± 1 SE.

<https://doi.org/10.1371/journal.pone.0204549.g001>

defense levels increased more steeply with access to dense Muslim colonies than under cleaner conditions, suggesting that low sanitation and ready access to Muslim subsidies acted in concert, i.e. synergistically affecting aggressiveness. Fourth, defense intensity declined with the green cover and was minimum at intermediate levels of built-up cover (Table 2A).

Finally, the number of fledglings produced by a pair was positively related to the defense intensity recorded for the same pair about two months earlier during incubation (Table 2B and Fig 2).

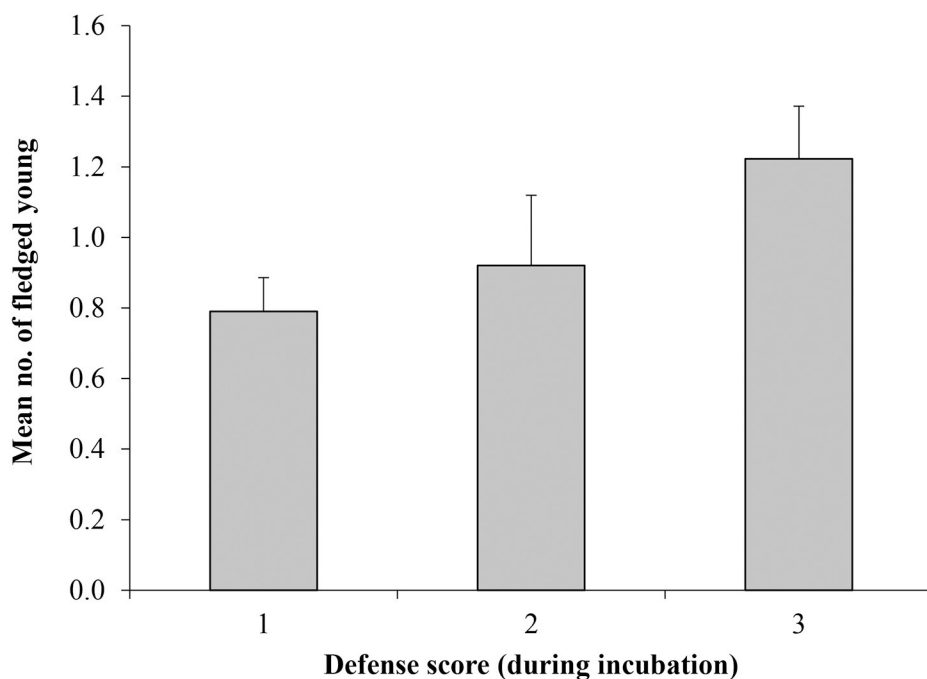


Fig 2. Number of fledglings produced by a pair in relation to the defense intensity exhibited by that pair two months earlier during incubation. Error bars represent ± 1 SE.

<https://doi.org/10.1371/journal.pone.0204549.g002>

Discussion

Kite defense levels progressively increased through the breeding cycle and reflected the number of offspring in the nest during each trial. These results confirmed those of several earlier studies e.g. [34–36] and suggested that parents tuned their defense response in relation to their parental investment, i.e. on the quantity and future survival prospects of their offspring, which increased through the breeding cycle. The fact that defense intensity early in the season predicted eventual young production months later, by the end of breeding, implied three non-exclusive possibilities: (1) parents could estimate the eventual likelihood of breeding success early in the season and set their defense accordingly; (2) aggressive nest defense lowered predation rates at the nest, with consequent benefits for young production; or (3) high quality individuals (e.g. healthier, or larger) were simultaneously more aggressive and better breeders, generating a positive association between two parameters separated by months in time. For example, kites that were more aggressive against humans could potentially be more aggressive against other more common nest predators such as crows or monkeys [21]. In support of this idea, in another study, nest defense by a falcon was experimentally shown to lower nest predation rates by corvids [35]. The above mix of associative and causative mechanisms produced results that are typical of avian nest defense studies e.g. [37, 38], suggesting that life in an urban setting did not disrupt the typical links between behavioural traits and vital rates found in avian populations.

More notably, despite constant close exposure to people, kite defense suggested that humans were not perceived as a neutral component of the urban landscape, but rather as a potential danger when they approached a nest. This implied a capability by kites to discriminate human attitudes and adjust their behaviour in a context-dependent manner, approaching people to very close quarters for feeding but fleeing and sometimes even attacking them when defending their offspring. Furthermore, defense levels varied through the city in relation to cultural ritual-feeding practices, refuse management and landscape composition. In particular, defense intensity was higher at sites that combined ready access to dense Muslim colonies (where kites are fed by humans by tossing meat-scraps at very close quarters) with poor sanitation (which promotes frequent feeding on anthropogenic waste close to people, e.g. at ephemeral garbage dumps also used by poor rag pickers digging for useful materials). This spatial association could be the result of three non-exclusive mechanisms: (a) frequent and reiterated, close contact with humans may have lowered fear, thus enhancing boldness and aggression; (b) sites close to ritual-feeding areas or with poor sanitation are over-selected by kites and thus likely occupied by higher quality individuals with higher parental investments [20], leading to higher defense intensity; and (c) bolder individuals may be more likely to withstand constant close proximity to humans and a bolder temperament is associated with greater aggression in some species e.g. [39]. Thus, individual quality, personality, habituation and motivation may have generated a spatial association between a behavioural strategy and a human cultural landscape, thus contributing to the growing appreciation of the importance of human cultural geographies for urban ecology e.g. [40–43].

While the exact mechanism remains uncertain, the behavioural response of kites to a perceived threat was finely tuned on the spatial arrangement of human activities and ritual practices, their consequent attitudes towards the birds, and their waste management organization. In turn, this would create a dynamic behavioural landscape, reflecting the underlying urban mosaic of resources, structures and human attitudes, to which kites will necessarily have to adapt and respond, as shown for species that colonized urban environments more recently [5].

The fact that aggression peaked at close human proximity suggested that close coexistence and habituation to people led to a loss of fear and heightened boldness towards humans, rather

than an enhanced capability to avoid them by keeping a “low profile” or learning to ignore them. Such dynamics may have been further favoured by the generally positive, religiously-based attitudes of Indian people towards wildlife, as reported by several studies e.g. [44–46].

Overall, these results confirm and extend earlier findings of more aggressive offspring defense by urban than rural individuals of a given species e.g. [47–49], suggesting that the route to close coexistence with humans is often accompanied by fine-grained, context-dependent strategies and trade-offs, rather than evolution of “blind tolerance” and indifference towards human activities [50]. In this sense, most animals making frequent contact with humans (through colonization of urban habitats, or through peri-urban encroachment) will likely need to develop cognitive capabilities and behavioural tactics that will enable them to exploit humans and cope with their omnipresent disturbance rather than learning to ignore them, in order to attain long-term coexistence e.g. [10, 51]. In turn, acquisition of such traits will likely be shaped by a two-way interaction between human perceptions, attitudes and practices on one part and daily experience and habituation to humans on the part of the animal. For synurbic species, like kites, at the high end of the spectrum of adaptation to an urban life, the above cited interaction may lead to behavioural and demographic traits fine-tuned not only on urban physical structures, but also on human cultural practices and attitudes, which for many species may become the most important, defining dimensions of their urban niche.

To date, most studies of animal behavioural responses to urbanization have focused on the comparison between urban and rural individuals, in order to draw inferences on the characteristics that enable or mediate the colonization of highly anthropogenic urban environments e.g. [7, 9, 10]. Here, we show that marked heterogeneity in behavioural responses to humans also continue to exist within cities and after centuries of initial urban colonization, suggesting further fine-tuning of behavioural traits on specific dimensions of the urban environment. In this sense, the urban-rural comparison does not target the end-result of colonization, but rather defines only the beginning of a hierarchical process of adaptation to humans, who are increasingly concentrated in cities. Thus, more research is needed on the fine-grained adjustments to urban structure and human culture by animals that are already in their mature stage of adaptation to an urban life.

Acknowledgments

We are grateful to Ben Sheldon, Chris Perrins, Tommaso Pizzari, Ujjwal Kumar, and the Director, Dean and research coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. We thank Drs. A. Margalida, W. Cresswell and two anonymous reviewers for helping us to improve a first draft of the manuscript. Delhi Police, and the Forest Departments of Delhi and Uttar Pradesh, Delhi Transport Corporation, Civic bodies of the Government of NCT of Delhi helped with legal permits, and the Director of the National Zoological Park of New Delhi gave access to study kites in the Park. Miranda House College and University of Delhi allowed access to their campus for nest monitoring. We express our most heartfelt gratitude to all the volunteers of the “Black Kite Project Group” from the University of Delhi (Sri Venkateswara and Deshbandhu Colleges), especially U. Gupta, H. Malhotra, A. Singh, P. Kumar, H. Singh, U. Nair and M. Singh, who provided essential field help, enthusiasm and cooperation in the environmental education of locally assembling crowds of curious people. Special thanks to our field assistants Laxmi Narayan, Prince Kumar and Poonam, who were the backbone of the field team. Finally, thanks to all the landowners, managers and government officials who patiently cooperated with our constant requests of access. We are thankful to the Publication Fee Assistance for financial support towards the publication of this manuscript.

Author Contributions

Conceptualization: Nishant Kumar, Qamar Qureshi, Fabrizio Sergio.

Data curation: Nishant Kumar.

Formal analysis: Nishant Kumar.

Funding acquisition: Nishant Kumar, Qamar Qureshi, Yadvendradev V. Jhala, Fabrizio Sergio.

Investigation: Nishant Kumar, Qamar Qureshi, Yadvendradev V. Jhala.

Methodology: Nishant Kumar, Fabrizio Sergio.

Project administration: Nishant Kumar, Qamar Qureshi, Yadvendradev V. Jhala.

Resources: Nishant Kumar, Qamar Qureshi, Yadvendradev V. Jhala, Andrew G. Gosler.

Software: Nishant Kumar.

Supervision: Qamar Qureshi, Yadvendradev V. Jhala, Andrew G. Gosler, Fabrizio Sergio.

Validation: Yadvendradev V. Jhala, Fabrizio Sergio.

Visualization: Nishant Kumar.

Writing – original draft: Nishant Kumar, Fabrizio Sergio.

Writing – review & editing: Nishant Kumar, Qamar Qureshi, Yadvendradev V. Jhala, Andrew G. Gosler, Fabrizio Sergio.

References

1. McDonnell MJ, Hahs AK. Adaptation and adaptedness of organisms to urban environments. *Annual Review of Ecology, Evolution, and Systematics*. 2015; 46: 261–280.
2. Miranda AC, Schielzeth H, Sonntag T, Partecke J. Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Global Change Biology*. 2013; 19:2634–2644. <https://doi.org/10.1111/gcb.12258> PMID: 23681984
3. Hahs AK, Evans KL. Expanding fundamental ecological knowledge by studying urban ecosystems. *Functional Ecology*. 2015; 29:863–867. <https://doi.org/10.1111/1365-2435.12488>
4. Chamberlain DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ, Gaston KJ. Avian productivity in urban landscapes: a review and meta-analysis. *Ibis*. 2009; 151(1):1–18. <https://doi.org/10.1111/j.1474-919X.2008.00899.x>
5. Evans KL, Hatchwell BJ, Parnell M, Gaston KJ. A conceptual framework for the colonisation of urban areas: the blackbird *Turdus merula* as a case study. *Biological Reviews*. 2010b; <https://doi.org/10.1111/j.1469-185x.2010.00121.x>
6. Smart J, Amar A, Sim IM, Etheridge B, Cameron D, Christie G, Wilson JD. Illegal killing slows population recovery of a re-introduced raptor of high conservation concern—The red kite *Milvus milvus*. *Biological Conservation*. 2010; 143:1278–1286. <https://doi.org/10.1016/j.biocon.2010.03.002>
7. Lowry H, Lill A, Wong BBM. Behavioural responses of wildlife to urban environments. *Biological Reviews*. 88:537–549. 2013; <https://doi.org/10.1111/brv.12012> PMID: 23279382
8. Blumstein DT. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*. 2006; 71:389–399. <https://doi.org/10.1016/j.anbehav.2005.05.010>
9. Møller AP. Flight distance of urban birds, predation, and selection for urban life. *Behavioral Ecology and Sociobiology*. 2008; 63:63–75. <https://doi.org/10.1007/s00265-008-0636-y>
10. Carrete M, Tella JL. Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PLoS One*. 2011; 6(4): e18859. <https://doi.org/10.1371/journal.pone.0018859> PMID: 21526193
11. Clucas B and Marzluff JM. Attitudes and actions toward birds in urban areas: human cultural differences influence bird behavior. *Auk*. 2012; 129:8–16. <https://doi.org/10.1525/auk.2011.11121>

12. Sprau P, Dingemanse NJ. An Approach to Distinguish between Plasticity and Non-random Distributions of Behavioral Types Along Urban Gradients in a Wild Passerine Bird. *Frontiers in Ecology and Evolution*. 2017; <https://doi.org/10.3389/fevo.2017.00092>
13. Francis RA, Chadwick MA. What makes a species sunurbi? *Applied Geography*. 2012; 32(2):514–521.
14. Gangoso L, Agudo R, Anadón JD, Manuel de la R, Suleyman AS, Porter R, et al. Reinventing mutualism between humans and wild fauna: insights from vultures as ecosystem services providers. *Conservation Letters*. 2012; 6:172–179. <https://doi.org/10.1111/j.1755-263x.2012.00289.x>
15. Kark S, Iwaniuk A, Schalimtzek A, Banker E. Living in the city: can anyone become an urban exploiter? *Journal of Biogeography*. 2007; 34:638–651. <https://doi.org/10.1111/j.1365-2699.2006.01638.x>
16. Evans KL, Chamberlain DE, Hatchwell BJ, Gregory RD, Gaston KJ. What makes an urban bird? *Global Change Biology*. 2010a; 17:32–44. <https://doi.org/10.1111/j.1365-2486.2010.02247.x>
17. Grimm NB, Grove JM, Pickett ST, Redman CL. Integrated Approaches to Long-Term Studies of Urban Ecological Systems. *BioScience*. 2000; https://doi.org/10.1007/978-0-387-73412-5_8
18. Lepczyk CA, Aronson MFJ, Goddard MA, Lerman SB, Malvor JS. Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. *Bioscience*. 2017; 67(9):799–807. <https://doi.org/10.1093/biosci/bix079>
19. Naoroji R. *Birds of prey of the Indian subcontinent*. Om Books International, New Delhi, India; 2007.
20. Kumar N, Gupta U, Jhala YV, Qureshi Q, Gosler AG, Sergio F. Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools. *Urban Ecosystems*. 2018; 21:339–349. <https://doi.org/10.1007/s11252-017-0716-8>
21. Kumar N, Mohan D, Jhala YV, Qureshi Q, Sergio F. Density, laying date, breeding success and diet of Black Kites *Milvus migrans govinda* in the city of Delhi (India). *Bird Study*. 2014; 61:1–8. <https://doi.org/10.1080/00063657.2013.876972>
22. Kumar N. A study of resource selection by Black Kites *Milvus migrans* in the National Capital Region. M.Sc. Thesis submitted to Wildlife Institute of India; Saurashtra University. Rajkot. Gujarat; 2013.
23. Census organization of India [Internet]. Census of India; c2011 [cited 25 Feb 2018]. Available from: <http://censusindia.gov.in/2011census>.
24. Pinault D. 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, Equinox Publishing Ltd, Bristol, CT, USA; 2008.
25. Taneja AV. Sainly animals: the shifting moral and ecological landscapes of North India. *Comparative Studies of South Asia, Africa and the Middle East*. 2015; 35:204–221.
26. Tabachnick BG, Fidell LS. *Using multivariate statistics*. HarperCollins, New York, USA; 1996.
27. Hedeker D, Gibbons RD. A Random-effects ordinal regression model for multilevel analysis. *Biometrics*. 1994; 50:933–944. PMID: 7787006
28. Agresti A. *Analysis of ordinal categorical data*, 2nd edn. Wiley, New York, USA; 2010.
29. Christensen RHB [Internet]. *Regression Models for Ordinal Data* [R package ordinal version 2015.6–28]. In: *The Comprehensive R Archive Network*; c2015 [cited 27 Sept 2017]. Available from: <http://cran.r-project.org/web/packages/ordinal/>.
30. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. *Mixed effects models and extensions in ecology with R*. Springer, New York, USA; 2011.
31. Crawley MJ. *The R book*. Wiley Press, Chichester, UK; 2013.
32. Grueber CE, Nakagawa S, Laws RJ, Jamieson IG. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 2011; 24: 699–711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x> PMID: 21272107
33. R Development Core Team [Internet]. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL; c2009 [cited 27 Sept 2018]. Available from: <http://www.R-project.org>
34. Hakkarainen H, Korpimäki E. Nest defence of Tengmalm's owls reflects offspring survival prospects under fluctuating food conditions. *Animal Behaviour*. 1994; 48:843–849.
35. Sergio F, Bogliani G. Nest Defense as Parental Care in the Northern Hobby (*Falco subbuteo*). *The Auk*. 2001; 118:1047. [https://doi.org/10.1642/0004-8038\(2001\)118\[1047:ndapci\]2.0.co;2](https://doi.org/10.1642/0004-8038(2001)118[1047:ndapci]2.0.co;2)
36. Møller AP, Nielsen JT. Parental defense of offspring and life history of a long-lived raptor. *Behavioral Ecology*. 2014; 25:1505–1512. <https://doi.org/10.1093/beheco/aru130>
37. Montgomerie RD, Weatherhead PJ. Risks and rewards of nest defence by parent birds. *Q Rev Biol*. 1988; 63: 167–187.

38. Redondo T. Avian Nest Defence: Theoretical Models and Evidence. *Behaviour*. 1989; 111:161–195. <https://doi.org/10.1163/156853989x00646>
39. Evans JE, Boudreau K, Hyman J. Behavioural syndromes in urban and rural populations of song sparrows. *Ethology*. 2010; 116: 588–595.
40. Alberti M. *Advances in urban ecology: integrating humans and ecological processes in urban ecosystems*. Springer, New York; 2008.
41. Forman RTT. *Urban ecology: science of cities*. Cambridge University Press, Cambridge, UK; 2014.
42. Pickett STA, Cadenasso ML, Childers DL, McDonnell MJ, Zhou W. Evolution and future of urban ecological science: ecology in, of, and for the city. *Ecosystem Health and Sustainability*. 2016; 2: e01229. <https://doi.org/10.1002/ehs2.1229>
43. Lepczyk CA, Warren PS, Machabée L, Kinzig AP, Mertig AG. Who feeds the birds? A comparison across regions. In: Lepczyk CA, Warren PS (eds) *Urban bird ecology and conservation*. University of California Press, Berkeley. 2012; pp 267–286. <https://doi.org/10.1525/california/9780520273092.003.0017>
44. Saberwal VK, Kothari A, Rangarajan M. *People, parks, and wildlife: towards coexistence*. Orient Longman, Delhi, India; 2001.
45. Bagchi S, Mishra C. Living with large carnivores: predation on livestock by the snow leopard (*Uncia uncia*). *Journal of Zoology*. 2006; 268:217–224. <https://doi.org/10.1111/j.1469-7998.2005.00030.x>
46. Karanth KK, Naughton-Treves L, Defries R, Gopalaswamy AM. Living with Wildlife and Mitigating Conflicts Around Three Indian Protected Areas. *Environmental Management*. 2013; 52:1320–1332. <https://doi.org/10.1007/s00267-013-0162-1> PMID: 24026255
47. Knight RL, Grout DJ, Temple SA. Nest-defense behavior of the American Crow in urban and rural areas. *Condor*. 1987; 89:175–177.
48. Kunca T, Yosef R. Differential nest-defense to perceived danger in urban and rural areas by female Eurasian sparrowhawk (*Accipiter nisus*). *PeerJ*. 2016; <https://doi.org/10.7717/peerj.2070> PMID: 27441105
49. Moroni E, Crivelaro AZ, Soares TL, Guillermo-Ferreira R. Increased behavioural responses to human disturbance in breeding Burrowing Owls *Athene cunicularia*. *Ibis*. 2017; 159: 854–859.
50. Dingemanse NJ, Kazem AJ, Réale D, Wright J. Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*. 2010; 25:81–89. <https://doi.org/10.1016/j.tree.2009.07.013> PMID: 19748700
51. Vincze E, Papp S, Preiszner B, Seress G, Bókony V, Liker A. Habituation to human disturbance is faster in urban than rural house sparrows. *Behavioral Ecology*. 2016; 27:1304–1313.
52. Newton I. *Population ecology of raptors*. Poyser, Berkhamstead, UK; 1979.
53. Knight RL, Temple SA. Why does intensity of avian nest defense increase during the nesting cycle? *Auk*. 1986; 103: 318–327.
54. Shea K, Roxburgh SH, Rauscher ES. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters*. 2004; 7(6): 491–508. <https://doi.org/10.1111/j.1461-0248.2004.00600.x>

Human-attacks by an urban raptor are tied to human subsidies and religious practices

Nishant Kumar, Yadvendradev Jhala, Qamar Qureshi, Andrew Gosler & Fabrizio Sergio

*Accepted for publication on December 27, 2018; in press, **Scientific Reports**.*



Abstract

Growing urbanization is increasing human-wildlife interactions, including attacks towards humans by vertebrate predators, an aspect that has received extremely scarce investigation. Here, we examined the ecological, landscape and human factors that may promote human-aggression by raptorial Black kites *Milvus migrans* in the 16-millions inhabitants' megacity of Delhi (India). Physical attacks depended on human activities such as unhygienic waste management, ritual-feeding of kites (mainly operated by Muslims), human density, and presence of a balcony near the nest, suggesting an association between aggression and frequent-close exposure to humans and derived food-rewards. Surprisingly, while more than 100,000 people could be at risk of attack in any given moment, attitudes by local inhabitants were strikingly sympathetic towards the birds, even by injured persons, likely as a result of religious empathy. These results highlight the importance of socio-cultural factors for urban biota and how these may radically differentiate the under-studied cities of developing countries from those of western nations, thus broadening our picture of human-wildlife interactions in urban environments. The rapid sprawling of urban and suburban areas with their associated food-subsidies is likely to increase proximity and exposure of large predators to humans, and vice versa, leading to heightened worldwide conflicts.

Keywords: ethnozoology; human-wildlife conflict; mitigation; raptors; urban management

SCIENTIFIC REPORTS

OPEN

Human-attacks by an urban raptor are tied to human subsidies and religious practices

Nishant Kumar^{1,2}, Yadvendradev V. Jhala², Qamar Qureshi², Andrew G. Gosler^{1,3} & Fabrizio Sergio⁴

Received: 20 August 2018

Accepted: 27 December 2018

Published online: 22 February 2019

Growing urbanization is increasing human-wildlife interactions, including attacks towards humans by vertebrate predators, an aspect that has received extremely scarce investigation. Here, we examined the ecological, landscape and human factors that may promote human-aggression by raptorial Black kites *Milvus migrans* in the 16-millions inhabitants megacity of Delhi (India). Physical attacks depended on human activities such as unhygienic waste management, ritual-feeding of kites (mainly operated by Muslims), human density, and presence of a balcony near the nest, suggesting an association between aggression and frequent-close exposure to humans and derived food-rewards. Surprisingly, while more than 100,000 people could be at risk of attack in any given moment, attitudes by local inhabitants were strikingly sympathetic towards the birds, even by injured persons, likely as a result of religious empathy. These results highlight the importance of socio-cultural factors for urban biota and how these may radically differentiate the under-studied cities of developing countries from those of western nations, thus broadening our picture of human-wildlife interactions in urban environments. The rapid sprawling of urban and suburban areas with their associated food-subsidies is likely to increase proximity and exposure of large predators to humans, and vice versa, leading to heightened worldwide conflicts.

There is growing interest in the interactions between human culture and animals, as evidenced by the rapid spread of studies in the field of ethnozoology^{1–3}. The need for integration of human socioeconomic and cultural variables into ecological research is particularly obvious in studies that focus directly on human-wildlife conflicts, or on expanding anthropogenic environments such as cities, where urban residents are confronted with a “novel” human-wildlife interface^{4–7}.

In particular, worldwide urban residents are experiencing a growing frequency of encounters with wildlife due to increasing urbanization, human encroachment of natural habitats, expanding greenspaces within cities, intentional feeding to attract wildlife, and growing adaptation of animal species to urban ecosystems^{8–10}. While close encounters may be beneficial in reconnecting urban people with ‘nature’^{11,12}, such increasing contacts are accompanied by an equally growing rate of human-wildlife conflicts, such as vehicle collisions, property damage, pet predation, disease transmission and even physical attacks on humans^{13–15}. Conflicts of this kind are typically difficult to manage because socio-political and cultural attitudes and perceptions often make mitigation controversial^{5,16}. This is especially pronounced in urban settings, which may pool together people with very different cultural backgrounds and with substantial differences in their interest or tolerance of wildlife, let alone of nuisance animals^{14,17,18}. Furthermore, urban animals may behave differently from their rural counterparts, thus requiring specially-designed mitigation measures¹⁹.

An extreme and sometimes dramatic form of human-wildlife conflict is represented by direct physical attacks on humans, which may cause psychological distress, diseases, injuries, sometimes severe or permanent ones, and even loss of life^{7,20–23}. Similarly to other forms of conflict, the frequency and severity of aggression on humans seem to be increasing in many urban areas^{24–27}. This creates an urgent need to know the potential drivers and risk

¹Edward Grey Institute of Field Ornithology, Department of Zoology; South Parks Road, University of Oxford, Oxford, OX1, 3PS, United Kingdom. ²Wildlife Institute of India, Post Box # 18, PIN- 248001, Chandrabani, Dehradun, (Uttarakhand), India. ³Institute of Human Sciences, School of Anthropology and Museum Ethnography, 58a Banbury Rd., Oxford, OX2 6QS, United Kingdom. ⁴Department of Conservation Biology, Estacion Biologica de Doñana-CSIC, C/Americo Vespucio 26, 41092, Sevilla, Spain. Correspondence and requests for materials should be addressed to N.K. (email: nishant.kumar@zoo.ox.ac.uk)



Figure 1. A Black kite takes off from its nest on a light pole to attack the photographer, who is standing on a balcony (Photo credit: F. Sergio).

factors underpinning the attacks, in order to devise mitigation strategies and avoid conflict, which might prejudice peoples' perceptions of and actions towards wildlife in general^{28–30}.

A special subset of these potentially-aggressive species is represented by vertebrate top predators, such as mammalian carnivores or birds of prey. Because of their armament, harm potential, and dangerous iconic nature in collective imagery, these species typically evoke more emotional responses and intolerance than other species^{31–33}, frequently leading to “hyper-perception of risk”⁵. For example, Kellert³⁴ showed that people tend to be more afraid of species that have the potential to harm them. Independently of perceptions, some of these predators have colonized many cities and increased dramatically in some urban areas in recent decades, sometimes reaching densities unparalleled in rural areas^{24,32,35–37}. In turn, this has increased encounters and conflict, sometimes with well demonstrated upturns in attack rates and even fatalities, frequently sensationalized by the public media^{24–27}. In many cases, increased aggression has been linked with intentional and unintentional human feeding of the predators, resulting in consequent loss of fear^{38–40}. Despite all the above, very few studies have examined the conditions that may predispose certain individuals to attack humans, and most of them have focused on mammals in rural areas^{7,41–43}. Thus, there is a great need for information from urban areas and other taxonomic groups to advance knowledge in this field. Here we assess the ecological, landscape and human factors that may promote aggression towards humans by raptorial Black Kites *Milvus migrans* (Fig. 1) in Delhi (India), a megacity of 16-million inhabitants, which hosts one of the largest concentrations of vertebrate predators of the world⁴⁴. In particular, we tested the hypothesis that individuals more exposed to human feeding and subsidies may be more likely to attack humans.

The Black Kite (hereafter “kite”) is a medium-sized, opportunistic predator and facultative scavenger. It is considered the most successful raptor in the world, due to its capability to withstand anthropogenic habitat change and even breed in high numbers alongside dense human populations within cities, especially in tropical areas⁴⁵. Throughout its distribution, there are reports of individuals snatching food from humans, sometimes in aggressive ways, up to the point of being considered a local nuisance^{46,47}. In India, the native, resident subspecies *M. m. govinda* is synurbic⁴⁸, i.e. it occurs almost exclusively in close association with humans in towns and cities⁴⁹. In Delhi, where this study was conducted, kites breed throughout the city, often a few meters from human habitation, and locally reach extremely high densities, thanks to the exploitation of human food subsidies facilitated by inefficient refuse disposal and by religious kite-feeding practices^{44,50}. These centuries-old religious offerings (hereafter termed ‘ritualized-feeding’) consist in throwing meat scraps into the air for the kites to catch and are made for a variety of reasons, such as asking for blessings and relief from sins and worries^{51,52}. Whilst meat-offering is practiced by a number of communities, in Delhi it is especially prevalent amongst members of 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. Breeding individuals of this kite population often dive-bomb, scratch and harm humans with their talons when these approach their nest, sometimes causing deep cuts (Fig. 1). At times, these injuries may require medical examination because of the potential of subsequent infections, given kites’ frequent foraging on rotting organic waste.

Explanatory variables in each model ^a	Degrees of freedom	AICc	Delta AICc	Model weight
Hygiene score + Breeding success	5	66.29	0.00	0.34
Balcony + Hygiene score + Breeding success + Access to Muslim colonies + Balcony * Access to Muslim colonies	8	67.77	1.48	0.16
Hygiene score + Breeding success + Access to Muslim colonies	6	68.08	1.79	0.14
Balcony + Hygiene score + Breeding success	6	68.18	1.89	0.13
Hygiene score + Urban cover + Breeding success	6	68.41	2.12	0.12
Human density + Hygiene score + Breeding success	6	68.48	2.19	0.11

Table 1. Top ranking (i.e. with $\Delta AICc < 3$) generalised linear mixed models with binomial errors and a logit link function testing the effect of environmental, urban and human variables on likelihood of aggressive attack against humans (attacking vs control pair) by a nesting kite pair (N = 204 trials from 72 independent territories). Territory-identity nested within plot-identity was fitted as a random effect to all models. See Supplementary Table S.1 for the description of explanatory variables. ^aVariables presented to the model: Number of people, Balcony, Urban cover, Green cover, Hygiene score, Human density, Access to Muslim colonies, Access to Muslim colonies * Hygiene score, Access to Muslim colonies * Urban cover, Access to Muslim colonies * Green cover, and Access to Muslim colonies * Balcony.

Variable	B $\pm$ SE	Z test	P value
Breeding Success	28.69 $\pm$ 7.33	3.91	<0.0001
Hygiene score	30.4 $\pm$ 7.9	3.86	0.0001
Access to Muslim subsidies	1.31 $\pm$ 4.1	0.32	0.75
Balcony	8.57 $\pm$ 7.77	1.1	0.27
Balcony * Access to Muslim colonies	17.19 $\pm$ 6.86	2.54	0.012
Human density	1.14 $\pm$ 0.19	5.94	<0.0001
Urban Cover	0.57 $\pm$ 7.46	0.08	0.94
Intercept	-76.2 $\pm$ 21.37	3.56	0.0003

Table 2. Model averaged coefficients for the explanatory variables that entered the top-ranking models of Table 1.

Results

To investigate the determinants of kites' attacks on humans, we recorded aggressive events during routine visits to kites breeding sites, in which nests were approached and examined by a team of three people in a standardized manner (see Methods). Kites were classified as attacking when they dive-bombed and made physical contact with any member of the research team. In the four years of research, the percentage of attacking pairs averaged 25.5% (range 18.0–37.7%), and attacking individuals were present at 36 (i.e. 31.9%) of 113 separate territories checked at least once for reproduction. Twenty-one of these 36 attacking pairs but none of the 36 non-attacking pairs had a history of past local attacks, as from interviews with local inhabitants ($\chi^2 = 15.09$, $P < 0.0001$), suggesting that pairs identified as aggressive by our trials were not responding to an unusual stimulus, but were already known to be problematic pairs well before our research activities. In all attacks during our trials, kites dive-bombed at high speed and tried to hit the target-person on the head, typically with the open hallux and closed phalanges, so as to either scratch or knock the target-person on the head. Due to escape movements, scratches were sometimes re-directed on the forehead or on the neck or shoulders. All attacks were from behind and never when a person was staring at a kite dive-bombing towards the group.

To investigate the potential drivers of aggression, we built a logistic mixed model discriminating between attacking and non-attacking kites on the basis of a series of ecological, landscape and human socio-religious variables (see Methods). In this model, the likelihood of attack increased with kite breeding success, with more human waste around the nest (higher hygiene score), with higher access to Muslim subsidies, with higher human density in the streets and with the presence of a close-by balcony facing the nest (Tables 1 and 2, Fig. 2). The interaction between balcony presence and access to Muslim subsidies was also important: kite aggression was more likely for pairs that had both a balcony close by and high access to Muslim subsidies (Fig. 3).

Discussion

Our results contribute to advance and integrate different fields of research such as ethnozoology, urban ecology and the resolution of human-wildlife conflicts. Below, we (1) explain the mechanisms that may generate the observed patterns and (2) discuss the importance of our findings for each of the above three disciplines.

Kite attacks on humans were not randomly distributed through the city and responded to a series of indicators of human activities, such as unhygienic management of waste disposal, Muslim ritual-feeding, and the intensity of human activity in the streets. This configuration of socio-religious features is preferred by the kites of Delhi because of its high food availability in the form of ritual subsidies and organic garbage⁵⁰ and may have promoted aggression in three non-exclusive ways. First, kites feeding on ritual subsidies or organic waste (frequently accomplished side by side with indigent people digging for useful materials) are frequently in close proximity to people,

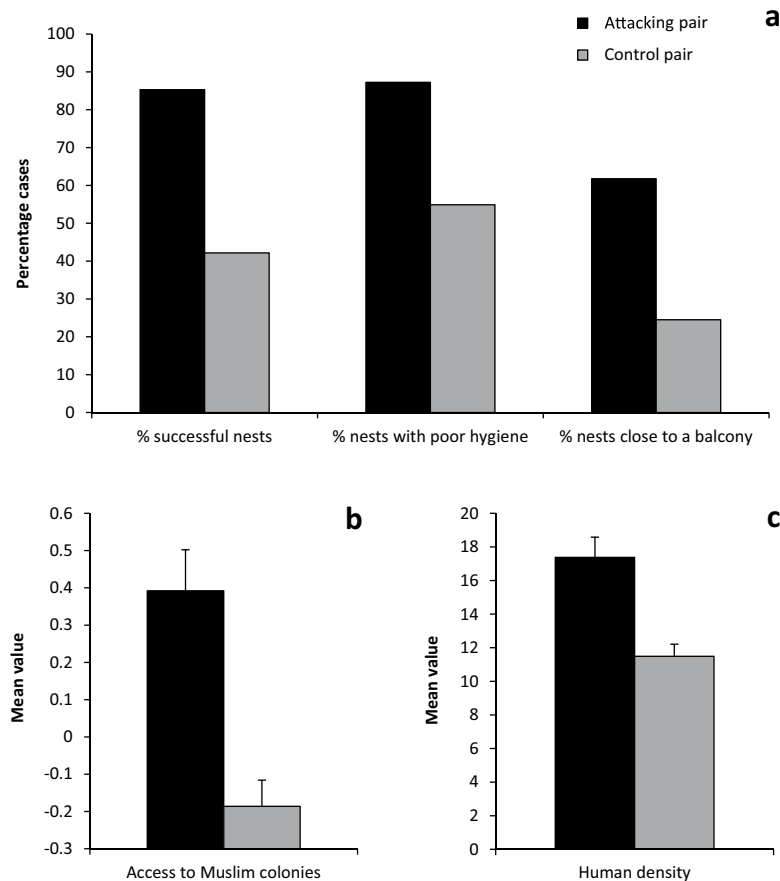


Figure 2. The likelihood of attacking humans by a breeding Black kite pair increased with: its breeding success (panel a, left bars), with more human waste around its nest (higher hygiene score, panel a, central bars), with the presence of a balcony in close proximity of the pair's breeding site (panel a, right bars), with higher access to ritual subsidies from Muslim colonies (panel b), and with higher human density in the streets of the nest surroundings (panel c). Error bars represent 1 SE.

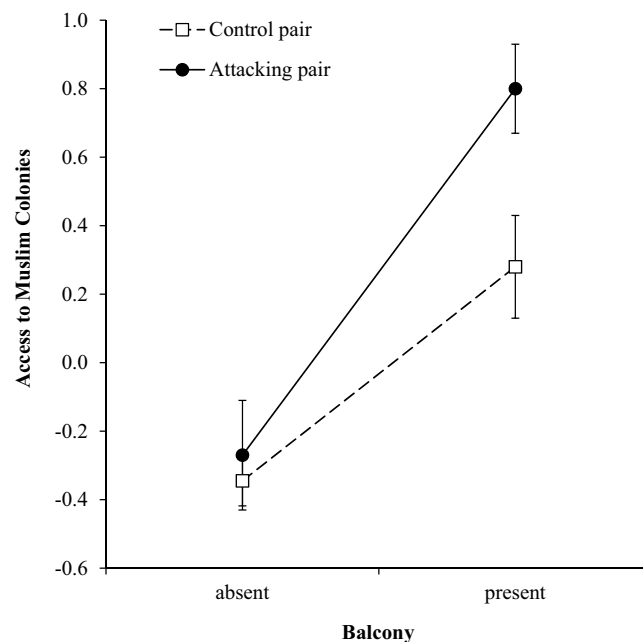


Figure 3. Likelihood of aggressive attack on humans by nesting Black kites in relation to access to ritual-feeding sites (Muslim colonies) and the presence of a balcony within 20m radius of the nest. Error bars represent 1 SE.

which may have lowered their fear of humans. Second, close proximity was frequently rewarded with food, which may have reinforced such loss of fear. Third, aggression varied with the interaction between access to Muslim ritual-subsidies and the presence of a balcony in the immediate proximity of the nest (Fig. 3). Thus, Muslim subsidies increased aggression-likelihood more markedly for pairs that nested in the immediate proximity of a balcony and, conversely, the presence of a balcony heightened aggression for pairs with ready access to Muslim subsidies. This suggests that peak aggression was promoted by the synergy of these two exposures to frequent and close encounters with humans.

In addition, human attacks were linked to successful reproduction. This could be promoted by two non-exclusive mechanisms: (1) parents could have a sense of the quality of their parental investment (e.g. based on their own or their offspring body condition) and defend more fiercely when success-prospects are high, as shown in other species^{53–55}; and (2) aggressive behaviour towards humans paralleled the capability to repel other more common nest predators, such as crows or monkeys⁴⁴, leading to a lower probability of nest failure from predation. Independently of motivational or causal mechanisms, if human-attacking pairs are more productive, there is a possibility that such behaviour could become more frequent in the population in the future, particularly so if aggression propensity were genetically inherited or culturally transmitted (e.g. by young kites emulating their parents' defense tactics once adult).

Implications for urban ecology. Implications for urban ecology were clear and profound. First, kite aggression did not respond to landscape composition or other classical ecological variables, but rather to a series of socio-religious and cultural features. This represents a clear-cut example of the importance of integrating human cultural factors into research programs in urban ecology. While human presence and action is one of the most defining characteristics of urban ecosystems⁴, few studies on urban animals explicitly incorporate human culture and perceptions into their design^{56,57}. When such aspects are tested, they are usually found to be key factors for urban ecology and conservation. For example, human socio-economic status has been shown to affect avian diversity, occurrence and distribution^{58–60}, while human perceptions of affinity/aversion towards certain animals varied across an urban-rural gradient, with important repercussions for potential conservation action⁶¹.

Second, some studies have shown that bolder, more aggressive individuals are more likely to colonize urban environments^{62–65}. These links have usually been shown in comparisons of urban vs rural populations. If we consider the propensity to attack humans observed in this study as a measure of boldness, then our data extend this urban-rural comparison to individual variation within a city. Under this scenario, boldness in human tolerance may continue to be a key modulator of urban adaptation and exploitation even long after the initial colonization of the urban environment.

Third, the occurrence of the attacks in a highly-subsidized and thus high-density animal population coexisting with a dense human population generated a problem of unusual magnitude. First of all, only 25–30% of kite pairs attacked humans, which compares with 19 and 73% of Australian magpies *Gymnorhina tibicen* and Masked lapwings *Vanellus miles*, two species also renowned for their attacks on humans in urban settings^{20,66}. However, even if only one in three or four pairs attacked humans, the local high density of kites over a very large area (average of 15 pairs/km²)⁴⁴ implies that Delhi could easily hold over 5600 aggressive pairs. If we further consider that human density is high in Delhi and that attacking pairs were disproportionately concentrated in areas of higher human density, several thousand people could be potentially exposed to kites' attacks every year. For example, during our tests of approximately 20 min duration, there were on average 18 people in the immediate proximity of the nest of an attacking pair. If this figure is representative, then multiplying it by 5600 aggressive pairs would imply that more than 101,000 people could be passing/standing within attacking-radius of an aggressive kite pair basically in every given moment of the day. Furthermore, most of the pairs that attacked us had a clear history of past attacks on local inhabitants, implying that our type of deliberate nest intrusion did not somehow exaggerate the extreme attacks that we recorded. Attacking individuals were 'problematic' already well before our activities. Conflicts of this magnitude and concentration would be unlikely in any rural setting and underline how urban ecosystems may pose novel challenges and require new approaches to wildlife management and conservation¹⁹.

Implications for research on human-wildlife conflict. This study confirmed and extended current knowledge on the drivers of human-attacks by vertebrate animals. First, habituation to human proximity and animal feeding have been frequently reported as drivers of aggression on humans by mammalian carnivores and primates^{38–40,42,67}. Our findings support these views, extend them to avian predators and thus suggest that they may represent generalized drivers of potential aggression across distantly related taxa. Second, human conflict with predators has often been associated with food scarcity driving low-quality, food-deprived individuals in close contact with humans^{7,66,68–71}. In our case, attacks were concentrated in optimal, preferred habitat, and perpetrated by more productive, likely higher-quality individuals. Such dynamics may be more typical of synanthropic urban predators, whose high-quality individuals may be drawn to an abundant food supply but get habituated to humans in the process of accessing it. While food availability in both cases may mediate aggression, its enactment by individuals of different quality and breeding-potential may have strong repercussions for future trends in aggression rates, with obvious forecasting and management implications. This confirms the importance of resource-distribution in wildlife-human conflicts^{10,72} and further remarks how the management of synanthropic or urban wildlife may require specially-designed techniques¹⁹.

Finally, social factors and cultural perceptions have been identified as important drivers of the intensity of human-wildlife conflict, but are seldom taken into consideration^{5,7,42,61,73,74}. Our results not only stressed the importance of socio-religious variables as key drivers of the conflict, but also show how they can enter the equally key human-part of conflict resolution. In fact, despite the above-reported magnitude of the problem, interviews with 140 persons encountered under the nests of attacking pairs uncovered extremely positive attitudes of local inhabitants towards the birds, even by individuals who were previously injured (authors' unpubl. data). Overall,

most people expressed fear for the attacks, as logically expected, but 100% of the respondents justified and showed explicit sympathy for the kites. Sympathy was motivated in two ways: (1) kites were protecting their offspring (i.e. doing their duty of good parents), and (2) humans have destroyed and degraded natural habitats and wildlife has no option but to live with humans, implying the ultimate fault was of people rather than kites. In turn, local communities, all of them of either the Islamic or the Hindu faith, tied such empathy to religious views about kites and about wildlife in general. Muslims mainly revered kites as sort of sacred, given their role of “winged emissaries” that metaphorically take away towards the sky their sins, worries, or prayers, symbolized by the meat offered during ritual-feedings^{51,52}. Hindus believe that a soul undergoes body transformations, that all life forms are thus connected to one ultimate god form and thus they respected kites as part of their wider tolerance to all wildlife species as god’s beings. Finally, positive attitudes were probably further promoted by the fact that (1) attacks only occurred during a minor, predictable part of the year (duration of about two months), (2) that most injuries were generally light due to local people learning to avoid certain sites, and (3) that people were usually well aware of the useful ecosystem service provided to their neighbourhood by kites, which in Delhi remove more than 3900 tons of organic waste per year (authors’ unpubl. data).

Whatever the underlying motivation, these positive attitudes clearly translated into actions. All people reported taking (non-harmful) action to avoid confrontations, which may further reinforce kite aggression through additional reward. This included avoiding the nest proximity, dissuading children from using the parks or certain sections of the park, or refraining from using the balcony until the nestlings fledged. Some schools and canteens have changed their rules to make children and customers eat their lunch inside the premises rather than outdoor close to an attacking pair. In one case, the husband of a woman who received a serious scratch on her face enclosed the balcony with a volleyball net in order to get protection while continuing to use the balcony. In all these cases, no attempts at retaliatory measures, such as nest removal or killing the birds, were ever noticed or reported. On few occasions, local inhabitants enquired the possibility that we could remove the nest, but strongly specifying that it would have to be done after the nestlings had fledged. They also asked information about whether there could be non-harmful ways to dissuade kites from nesting at specific locations and about how to behave so as to avoid being attacked. Note that such extreme tolerance, even after injury, would be extremely unlikely by denizens of the western world, where conflicts of similar kind often end up in court after retaliatory nest removals or illegal killings^{7,75} and where urban people are often reported as disconnected from nature and profoundly puzzled by conflicts with wildlife, frequently seen as a nuisance to remove^{10,18,76,77}. Finally, to date the few studies that have examined the role of human religion, ethnicity, or social factors in human-wildlife conflict have shown how they can shape human attitudes and perceptions and thus intervene on the human side of the conflict^{5,7,42,61,73,74}. In our case, we show that they can also affect the animal side of the conflict-interaction by shaping animal aggression through reward and habituation, thus confirming and extending their importance.

Implications for ethnozoology and the importance of human cultural factors. Human socio-cultural factors permeated all results and allowed more realistic insights into the drivers of a human-wildlife conflict. In particular, kite attacks on humans responded to a geography of human religion, hygiene and poverty, and were concentrated within the productive sector of the kite population located at the high-end of the human-exploitation axis. Notably, kite behaviour was keenly adjusted to humans, tolerating them at close range when feeding but attacking them when provoked, while humans equally responded to kite behaviour, encouraging their ecosystem service function and avoiding them without retaliation when attacked. In this sense, kites and humans could be contextualized as participants in a “coupled-system” where each of the two actors co-shaped each other’s socio-ecological space through repeated interactions, a phenomenon already suggested for other species^{78–81}. Human culture was thus key to identifying drivers of attacks and problematic sectors of the city. It also intervened to alleviate the conflict, as current evidence suggested that, at present, the aesthetic, cultural, spiritual and ecosystem-service benefits offered by kites clearly outweighed the local, albeit diffuse discomfort provided by aggressive individuals. This highlights a growing appreciation of the value of intangible benefits provided by wildlife to humans^{12,74,82,83}, but most of all, it shows how ethnozoological approaches can improve ecological insight and bridge the gap between different disciplines such as behavioural ecology, wildlife management and urban ecology through direct incorporation of human socio-cultural aspects^{2,3}. In fact, human-wildlife conflicts have been identified as prime examples of research and management activities where incorporation of socio-cultural tools is direly needed^{3,4}. In conclusion, given that many predatory vertebrates are likely to be attracted by subsidies from a growing human population worldwide⁸⁴, conflicts promoted by close exposure to humans, as portrayed here, are likely to increase.

Methods

Ethics statement. This research is part of a larger and long-term study on the demography of Black Kites in Delhi. We received the permits to conduct the fieldwork from the office of the Additional Principal Chief Conservator of Forests (APCCF), the Government of the National Capital Territory of Delhi under the provisions of the Wildlife Protection Act, 1972 (permit number: CF/LC/105/07/HQ/10504-8). The Training, Research, and Academic Council (TRAC) of the Wildlife Institute of India, Dehradun (WII), gave bioethical approval for the research protocols. We performed all methods in accordance with the relevant guidelines and regulations laid out by TRAC WII with respect to study animal and human participants. We also sought informed consent from all the participants (or their legal guardians) for the semi-structured interviews (see below). We took all precautions to ensure researcher and animal safety, and maintained anonymity of the human respondents at all the stages of data recording during the field trials. All members of the field team were regularly administered with preventive vaccination, they wore thick hats/helmets and appropriate protective clothing so as to ensure safety.

Study Area. Delhi is a megacity of more than 16 million inhabitants, covering an area of 1500 km² and in constant expansion⁸⁵. 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. These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries^{51,52}. Whilst meat-offering is practiced by a number of communities, in Delhi it is especially prevalent amongst members of 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 retains reasonable green cover, thus providing abundant nesting habitat for kites⁸⁶.

Fieldwork procedures and statistical analysis. Data on attacks were collected during nest-checks in 2013–2016, conducted at 20 plots randomly scattered throughout the city in order to cover all its possible urban settings, from semi-natural to extremely built-up sites (see^{44,50} for details of plots and nest checks). On each occasion, nests were visited in a standardised manner: a team of three people approached the nest directly from a point approximately 50 m from the nest, chosen to be clearly visible to a kite perched in the nest area. One person (always the same one) then proceeded to climb the nest. A kite pair was classified as attacking when either of the two parents dive-bombed and made physical contact with any member of the team. To examine the characteristics that may affect the likelihood of aggression, we compared attacking and non-attacking pairs in the following manner. First, for each pair that attacked us, we chose a non-attacking pair that: (1) had eggs or chicks of similar age, (2) that was checked in the same year and on the same or preceding-following day, (3) that had received a similar number of previous visits by our team, and (4) that had a similar tree-arrangement configuration (nest in an isolated tree, line of trees, parkland or continuous woodland). This allowed us to investigate aggression while removing the potentially confounding effects of year, date, breeding stage, previous visit and local habitat-structure. Second, for all attacking and non-attacking pairs we collected a number of landscape and human variables (Supplementary Table S.1), based on our knowledge of kite ecology and of a previous study on habitat preferences by Delhi kites⁵⁰. These variables estimated the structure and composition of the urban landscape around the nests, their local availability of organic garbage, their access to Muslim ritual-subsidies, the local density of humans around the nest and in the surrounding streets, and the close exposure to human presence through the presence-absence of an open balcony within 20 m of the nest (details in Supplementary Table S.1). Thus, they characterized each pair on the basis of its surrounding urban characteristics, food availability, and exposure to humans as well as their subsidies. Third, we used a logistic mixed model⁸⁷, with pair-identity nested within plot-identity, to discriminate between attacking and non-attacking pairs on the basis of the landscape and human variables. To reduce collinearity and the number of variables presented to multivariate models, we employed the method of variable reduction proposed by Green⁸⁸. In this method, pairs of strongly intercorrelated variables ($r > 0.6$) are considered as estimates of a single underlying factor. Only one of the two is retained for analysis, usually the one likely to be perceived as more important by the study organism. Of the remaining variables, only those for which significant univariate differences ($P < 0.1$) were detected between attacking and non-attacking pairs were included in the logistic model (Supplementary Table A.2). Univariate differences were carried out by means of t-tests and χ^2 tests. Model building was implemented through an information-theoretic approach, following recommendations by^{89–91}. We used the “dredge” function of the MuMIn package to rank competing models on the basis of their weight and AICc⁸⁹. Models within 3 AICc units of the top model were selected for model averaging, implemented through the MuMIn package. All the analyses were performed through R 3.4.3⁹².

Finally, to gain an understanding of the extent and impact of attacks on local communities, we approached and interviewed all the people we encountered during our trials in the immediate proximity of the nests of attacking and non-attacking pairs ($N = 278$ interviews). This allowed us to test whether pairs that attacked us also had a higher probability of previously attacking local people, i.e. before and independently of our activities. Detailed analysis of the interviews will be reported elsewhere, but in the Discussion we delineate the main local opinions qualitatively, in order to place the conflict in the context of local attitudes. Throughout, all tests are two-tailed, statistical significance was set at ≤ 0.05 and means are given with 1 SE. The dataset of the current study is available on reasonable request from the corresponding author.

Data Availability

Given that a part of the data is funded by a Foundation who has shared possession of the generated datasets, the data for the manuscript are available upon reasonable request from the authors.

References

1. Tidemann, S. & Gosler, A.G. *Ethno-ornithology: birds, indigenous people, culture and society*. (Earthscan, 2010).
2. Alves, R. R. N. Relationships between fauna and people and the role of ethnozoology in animal conservation. *Ethnobiol. Conserv.* **1**, 1–69 (2012).
3. Alves, R. R. N. & Albuquerque, U. P. *Ethnozoology: animals in our lives*. (Elsevier, 2018).
4. Alberti M. *Advances in urban ecology: integrating humans and ecological processes in urban ecosystems*. (Springer, 2008).
5. Dickman, A. J. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Anim. Conserv.* **13**, 458–466 (2010).
6. Redpath, S. M. *et al.* Understanding and Managing conservation conflicts. *Trends Ecol. Evol.* **28**, 100–109 (2013).
7. Torres, D. F., Oliveira, E. S. & Alves, R. R. N. Conflicts between humans and terrestrial vertebrates: a global review. *Trop. Conserv. Sci.* **11**, 1–15 (2018a).
8. Marzluff, J. *et al.* (Eds). *Urban ecology: an international perspective on the interaction between humans and nature*. (Springer, 2008).
9. Gaston, K. J. *Urban ecology*. (Cambridge University Press, 2010).

10. Soulsbury, C. D. & White, P. C. L. Human-wildlife interactions in urban areas: a review of conflicts, benefits and opportunities. *Wildl. Res.* **42**, 541–553 (2015).
11. Hosey, G. & Melfi, V. Human-animal interactions, relationships and bonds: a review and analysis of the literature. *Int. J. Comp. Psychol.* **27**, 117–142 (2014).
12. Cox, D. T. C. & Gaston, K. J. Urban bird feeding: connecting people with nature. *PLoS ONE* **11**(7), e0158717, <https://doi.org/10.1371/journal.pone.0158717> (2016).
13. Conover, M. R. *Resolving human-wildlife conflicts: the science of wildlife damage management*. (CRC Press, 2002).
14. Hadidian, J. Wildlife in U.S. cities: managing unwanted animals. *Animals* **5**, 1092–1113 (2015).
15. Adams, C. E. *Urban wildlife management*. (CRC Press, 2013).
16. Messmer, T. A. The emergence of human-wildlife conflict management: turning challenges to opportunities. *Int. Biodeterior. Biodegradation* **45**, 97–102 (2000).
17. Conover, M. R. Wildlife management by metropolitan residents in the United States: practices, perceptions, costs, and values. *Wildl. Soc. Bull.* **25**, 306–311 (1997).
18. Bjerke, T. & Østdahl, T. Animal-related attitudes and activities in an urban population. *Anthrozoös* **17**, Iss. 2, <https://doi.org/10.2752/089279304786991783> (2004).
19. Ditchkoff, S. S., Saafeld, S. T. & Gibson, C. J. Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosyst.* **9**, 5–12 (2006).
20. Jones, D. & Thomas, L. Attacks on humans by Australian magpies: management of an extreme suburban human-wildlife conflict. *Wildl. Soc. Bull.* **27**, 473–478 (1999).
21. Kofron, C. P. Attacks to humans and domestic animals by the southern cassowary (*Casuarius casuarius johnsonii*) in Queensland, Australia. *J. Zool.* **249**, 375–381 (1999).
22. Kushnir, H., Leitner, H., Ikanda, D. & Packer, C. Human and ecological risk factors for unprovoked lion attacks on humans in south-eastern Tanzania. *Human Dim. Wildl.* **15**, 315–331 (2010).
23. Sundarshan, M. K. *et al.* Assessing the burden of human rabies in India: results of a national multi-center epidemiological survey. *Int. J. Infect. Dis.* **11**, 29–35 (2017).
24. Timm, R. M., Baker, R. O., Bennett, J. R. & Coolahan, C. C. Coyote attacks: an increasing suburban problem. *Trans. North Am. Wildl. Nat. Res. Conf.* **69**, 67–88 (2004).
25. Siemer, W. F., Hart, S., Decker, D. J. & Shanahan, J. E. Factors that influence concern about human-black bear interactions in residential settings. *Human Dim. Wildl.* **14**, 185–197 (2009).
26. Thornton, C. & Quinn, M. S. Coexisting with cougars: public perceptions, attitudes, and awareness of cougars on the urban-rural fringe of Calgary, Alberta, Canada. *Human-Wildlife Conflicts* **3**, 282–295 (2009).
27. Bhatia, S., Athreya, V., Grenyer, R. & MacDonald, D. W. Understanding the role of representations of human-leopard conflict in Mumbai through media-content analysis. *Conserv. Biol.* **27**, 588–594 (2013).
28. St John, F. A. V. *et al.* Identifying indicators of illegal behaviour: carnivore killing in human-managed landscapes. *Proc. R. Soc. B.* **279**, 804–812 (2011).
29. Dickman, A. J., Hazzah, L., Carbone, C. & Durant, S. M. Carnivores, culture and ‘contagious’ conflict: multiple factors influence perceived problems with carnivores in Tanzania’s Ruaha landscape. *Biol. Conserv.* **178**, 19–27 (2014).
30. Hazzah, L., Bath, A., Dolrenry, S., Dickman, A. & Frank, L. From attitudes to actions: predictors of lion killing by Maasai warriors. *PLoS ONE* **12**(1), e0170796 (2017).
31. Fascione, N., Delach, A. & Smith, M. E. *People and predators: from conflict to coexistence*. (Island Press, 2004).
32. Gehrt, S. D., Riley, S. P. D. & Cypher, B. L. *Urban carnivores: ecology, conflict and conservation*. (The Johns Hopkins University Press, 2010).
33. Elliot, E. E., Vallance, S. & Molles, L. E. Coexisting with coyotes (*Canis latrans*) in an urban environment. *Urban Ecosyst.* **19**, 1335–1350 (2016).
34. Kellert, S. R. American attitudes toward and knowledge of animals: an update. *International Journal for the Study of Animal problems* **1**, 87–119 (1980).
35. Bird, D., Varland, D. & Negro, J. J. *Raptors in human landscapes*. (Academic Press, 1996).
36. Rutz, C. The establishment of an urban bird population. *J. Anim. Ecol.* **77**, 1008–1019 (2008).
37. Bateman, P. W. & Fleming, P. A. Big city life: carnivores in urban environments. *J. Zool.* **287**, 1–23 (2012).
38. McCullough, D. R. Behavior, bears, and humans. *Wildl. Soc. Bull.* **10**, 27–33 (1982).
39. Bounds, D. L. & Shaw, W. W. Managing coyotes in U.S. national parks: human-coyote interactions. *Natural Areas Journal* **14**, 280–284 (1994).
40. Thompson, J., Shirreffs, L. & McPhail, I. Dingoes on Fraser Island: tourism dream or management nightmare. *Human Dim. Wildl.* **8**, 37–47 (2003).
41. Nyhus, P. J. & Tilson, R. Characterizing human-tiger conflict in Sumatra, Indonesia: implications for conservation. *Oryx* **38**, 68–74 (2004).
42. Hockings, K. J., Yamakochi, G., Kabasawa, A. & Matsuzawa, T. Attacks on local persons by chimpanzees in Bossou, Republic of Guinea: long-term perspectives. *Am. J. Primatol.* **72**, 887–896 (2010).
43. Kushnir, H. *et al.* Using landscape characteristics to predict lion attacks on humans in south-eastern Tanzania. *Afr. J. Ecol.* **52**, 524–532 (2014).
44. Kumar, N., Mohan, D., Jhala, Y. V., Qureshi, Q. & Sergio, F. Density, laying date, breeding success and diet of Black Kites *Milvus migrans* in the city of Delhi (India). *Bird Study* **61**, 1–8 (2014).
45. Ferguson-Lees, J. & Christie, D. A. *Raptors of the world*. (Houghton Mifflin Company, 2001).
46. Parker, J. W. Raptor attacks on people. *J. Raptor Res.* **33**, 63–66 (1999).
47. Galbreath, D. M., Ichinose, T., Furutani, T., Yan, W. & Higuchi, H. Urbanization and its implication for avian aggression: a case study of urban black kites (*Milvus migrans*) along Sagami Bay in Japan. *Landscape Ecol.* **29**, 169–178 (2014).
48. Francis, R. A. & Chadwick, M. A. What makes a species synurbic? *Applied Geography* **32**, 514–521 (2012).
49. Naoroji, R. *Birds of prey of the Indian subcontinent*. (Christopher Helm/A&C Black Publishers Ltd., 2006).
50. Kumar, N. *et al.* 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 (2018).
51. Pinault, D. 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. Pinault, D.), 108–121 (Equinox Publishing Ltd, 2008).
52. Taneja, A. V. Sainly animals: the shifting moral and ecological landscapes of North India. *Comparative Studies of South Asia, Africa and the Middle East* **35**, 204–221 (2015).
53. Montgomerie, R. D. & Weatherhead, P. K. Risks and rewards of nest defence by parent birds. *Quarter. Rev. Biol.* **63**, 167–187 (1988).
54. Redondo, T. Avian nest defence: theoretical models and evidence. *Behaviour* **111**, 161–195 (1989).
55. Sergio, F. & Bogliani, G. Nest defense as parental care in the Northern Hobby. *Auk* **118**, 1047–1052 (2001).
56. Grimm, N. B., Steward, J. M. G., Pickett, T. A. & Redman, C. L. Integrated approaches to long-term studies of urban ecosystems. *BioScience* **50**, 571–584 (2000).
57. Liu, J. *et al.* Complexity of coupled human and natural systems. *Nature* **31**, 1513–1516.

58. Shaw, L. M., Chamberlain, D. & Evans, M. The House Sparrow *Passer domesticus* in urban areas: reviewing a possible link between post-decline distribution and human socioeconomic status. *J. Ornithol.* **149**, 293–299 (2008).
59. Van Heezig, Y. & Hight, S. R. Socio-economic-driven differences in bird-feeding practices exacerbate existing inequities in opportunities to see native birds in cities. *J. Urban Ecol.* <https://doi.org/10.1093/jue/jux011> (2017).
60. Van Heezig, Y., Freeman, C., Porter, S. & Dickinson, K. J. M. Garden size, householder knowledge, and socio-economic status influence plant and bird diversity at the scale of individual gardens. *Ecosystems* **16**, 1442–1454 (2013).
61. de Oliveira, J. V., de F. Lopes, S., Barboza, R. R. D. & Alves, R. R. N. To preserve, or not to preserve, that is the question: urban and rural student attitudes towards wild vertebrates. *Environ. Dev. Sustain.*, <https://doi.org/10.1007/s10668-018-0083-5> (2018).
62. Möller, A. P. Flight distance of urban birds, predation, and selection for urban life. *Behav. Ecol. and Socio.* **63**(1), 63–75 (2008).
63. Evans, J. E., Boudreau, K. & Hyman, J. Behavioural syndromes in urban and rural populations of song sparrows. *Ethology* **116**, 588–595 (2010).
64. Carrete, M. & Tella, J. L. Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PLoS One* **6**(4), e18859 (2011).
65. Lowry, H. & Wong, B. B. M. Behavioural responses of wildlife to urban environments. *Biol. Rev.* **88**, 537–549 (2012).
66. Lewis, D. L. *et al.* Foraging ecology of black bears in urban environments: guidance for human-bear conflict mitigation. *Ecosphere* **6**, 1–18 (2015).
67. Fa, J. E. Visitor-directed aggression among the Gibraltar macaques. *Zoo Biol.* **11**, 43–52 (1992).
68. Patterson, B., Kasiki, S. M., Selempo, E. & Kays, R. W. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Park, Kenya. *Biol. Conserv.* **119**, 507–516 (2004).
69. Graham, K., Beckerman, A. P. & Thirgood, S. Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. *Biol. Conserv.* **122**, 159–71 (2005).
70. Murray, M. H. & St. Clair, C. C. Predictable features attract urban coyotes to residential yards. *J. Wildl. Manage.* **81**, 593–600 (2017).
71. Torres, D. F., Oliveira, E. S. & Alves, R. R. N. Understanding human-wildlife conflicts and their implications in: *Ethnozoology: animals in our lives* (ed. Alves, R. R. N. & Albuquerque, U. P.), 421–445 (Elsevier, 2018b).
72. Blackwell, B. F. *et al.* No single solution: application of behavioural principles in mitigating human-wildlife conflict. *Anim. Behav.* **120**, 245–254 (2016).
73. Hazzah, L., Mulder, B. M. & Frank, L. Lions and warriors: social factors underlying declining African lion populations and the effect of incentive-based management in Kenya. *Biol. Conserv.* **142**, 2428–2437 (2009).
74. Kinsky, R. & Knight, A. T. Key factors driving attitudes towards large mammals in conflict with humans. *Biol. Conserv.* **17**, 93–105 (2014).
75. Lees, D. *et al.* Swooping in the suburbs: parental defence of an abundant aggressive urban bird against humans. *Animals* **3**, 754–766 (2013).
76. Sterba, J. *Nature wars: the incredible story of how wildlife comebacks turned backyards into battlegrounds*. (Crown Publishers, 2012).
77. Miller, J. R. Biodiversity conservation and the extinction of experience. *Trends Ecol. Evol.* **20**, 430–434 (2005).
78. Marzluff, J. M. & Angell, T. Cultural coevolution: how the human bond with crows and ravens extends theory and raises new questions. *J. Ecol. Anthropol.* **9**, 69–75 (2005).
79. Clucas, B. & Marzluff, J. M. Coupled relationships between humans and other organisms in urban areas In: *Urban ecology: patterns, processes, and applications* (ed. Niemelä, J.), 135–147 (Oxford University Press, 2011).
80. Riley, E. P. & Priston, N. E. C. Macaques in farms and folklore: exploring the human-nonhuman primate interface in Sulawesi, Indonesia. *Am. J. Primatol.* **71**, 825–839 (2010).
81. Fuentes, A. Ethnoprimateology and the anthropology of the human-primate interface. *Annu. Rev. Anthropol.* **41**, 101–117 (2012).
82. Maller, C., Townsend, M., Prior, A., Brown, P. & St. Leger, L. Healthy nature healthy people: ‘contact with nature’ as an upstream health promotion intervention for populations. *Health Promotion International* **21**, 45–54 (2006).
83. Keniger, L. E., Gaston, K. J., Irvine, K. N. & Fuller, R. A. What are the Benefits of Interacting with Nature? *Journal of Environmental Research and Public Health* **10**, 913–935 (2013).
84. Newsome, T. M. *et al.* The ecological effects of providing resource subsidies to predators. *Global Ecol. Biogeog.* **24**, 1–11 (2015).
85. Census Organisation of India. Office of the Registrar General & Census Commissioner, India, <http://censusindia.gov.in/2011census> (2011).
86. Paul, S. & Nagendra, H. Vegetation change and fragmentation in the mega city of Delhi: mapping 25 years of change. *Appl Geogr.* **58**, 153–166 (2015).
87. Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. *Mixed effects models and extensions in ecology with R*. (Springer, 2009).
88. Green, R. H. *Sampling design and statistical methods for environmental biologists*. (John Wiley & Sons, 1979).
89. Grueber, C. E., Nakagawa, S., Laws, R. J. & Jamieson, I. G. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* **24**, 699–711 (2011).
90. Richards, S. A., Whittingham, M. J. & Stephens, P. A. Model selection and model averaging in behavioural ecology: the utility of IT-AIC framework. *Behav. Ecol. Sociobiol.* **65**, 77–89 (2011).
91. Galipaud, M., Gillingham, M. A. F., David, M. & Dechaume-Moncharmont, F. Ecologists overestimate the importance of predictor variables in model averaging: a plea for cautious interpretations. *Methods Ecol. Evol.* **5**, 983–991 (2014).
92. R Development Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna (2017).

Acknowledgements

We thank Dr. R. Dor and two anonymous reviewers for constructive comments that greatly improved the manuscript, and Ujjwal Kumar and the Director, Dean and Research Coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. Delhi Police, and the Forest Departments of Delhi and Uttar Pradesh, Delhi Transport Corporation, Civic bodies of the Government of NCT of Delhi helped with legal permits, and the Director of the National Zoological Park of New Delhi gave access to study kites in the Park. Miranda House College and University of Delhi allowed access to their campus for nest monitoring. We thank Laxmi Narayan, Prince Kumar, Poonam and all the members of the “Black Kite Project Group” for help in the field, especially U. Gupta, H. Malhotra, A. Singh, P. Kumar, H. Singh, U. Nair and M. Singh. Special thanks to R. Naoraji and K. Srivastava for constant support. The project was funded by the Raptor Research and Conservation Foundation (Mumbai) and by the Govt. of India, Ministry of Environment, Forest and Climate Change. NK was funded by the Felix Scholarship Trust and Somerville College, Oxford University and FS by project CGL2015- 69445-P of the Spanish Ministry of Economy and Competitiveness with Feder Funds.

Author Contributions

N.K., Y.V.J., Q.Q., A.G.G. and F.S. conceived the ideas and designed methodology; N.K., F.S. collected the data; N.K. analyzed the data; N.K., F.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Additional Information

Supplementary information accompanies this paper at <https://doi.org/10.1038/s41598-019-38662-z>.

Competing Interests: The authors declare no competing interests.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2019

Supplementary Tables

Supplementary Table S.1. Ecological, landscape and human variables used to characterize Black kite attacking and non-attacking pairs within the city of Delhi (India).

Variable	Description
Number of people	Number of people (not belonging to the field-team) within 50 m of the nest at the beginning of the attack trial (e.g. sitting in a park, playing, walking in the street, etc.)
Number of offspring	Number of eggs or chicks in the nest at the time of the kite attack trial
Breeding Success	Categorical variable: 0 = failed breeding attempt, 1 = successful breeding attempt. An attempt was classed as successful if the pair managed to raise at least one nestling to fledging age (40-48 days old).
NND5 (m)	Mean of the distance to the five closest kite neighbours
Territories within 200 m	Number of territories occupied within 200 m of the target nest
Colony size	Number of nests within the kite colony
Balcony	Categorical variable: 0 = absence, 1 = presence of a balcony within 20 m of the sampled nest
Index of road density	Number of asphalted roads crossed by a 500 m north-south and a 500 m east-west transect crossing each other on the nest
Urban cover	Percentage area covered by built-up structures (buildings, roads, parking lots, or any other impervious surface) within 500 m of the nest
Green cover	Percentage area covered by shrub/tree vegetation within 500 m of the nest
Hygiene score	Level of sanitation: 1 = clean areas; 2 = areas under poor waste management regime ^a
Human density	Average number of people walking within 2m of a stationary observer during 5 min at 10 locations randomly plotted within 200 m of the nest ^b
Access to Muslim subsidies	First component (PC1) of a principal component analysis on Muslim density and on the proximity to the three closest Muslim colonies (following Kumar et al. ³⁹).

^a Categorical variable with two levels: 1 = efficient waste disposal with very scarce or no organic refuse in the streets; 2 = abundant and widespread refuse in the streets throughout the area, either in small frequent piles, in illegal ephemeral dumps, or as individual items scattered a bit of everywhere through all streets (following Kumar et al.⁵⁰).

^b Counts were only operated between 10:00-17:00 hrs and avoided during atypical, momentary peak periods of human traffic, such as exits from work or schools, in order to maintain consistency across sites (following Kumar et al.⁵⁰).

Supplementary Table S.2. Mean (± 1 SE) estimates of variables measured at 36 Black Kite pairs that attacked humans for nest defense and at 36 control pairs for which no attacks were observed. Differences between the two samples were tested by means of t-tests, or χ^2 tests for categorical variables. Symbols: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Variable	Attacking pairs	Non-attacking pairs
Offspring number ***	1.89 ± 0.10	1.32 ± 0.10
Breeding Success ^{a, b} ***	85.29 %	42.15 %
Index of road density ^b	7.52 ± 0.24	7.40 ± 0.34
Urban cover ^b ***	0.46 ± 0.02	0.35 ± 0.02
Green cover ^b **	0.23 ± 0.01	0.31 ± 0.02
Balcony ^{b, c} ***	61.76 %	24.51 %
NND5 (m) *	156.31 ± 10.75	197.58 ± 16.66
Territories within 200 m	9.89 ± 0.61	8.85 ± 0.58
Colony size	5.67 ± 0.34	4.92 ± 0.31
Number of people ^b ***	18.05 ± 1.47	8.96 ± 0.83
Hygiene score ^{b, d} ***	87.25 %	54.90 %
Human density ^b ***	17.38 ± 1.19	11.49 ± 0.72
Access to Muslim subsidies ^b **	0.39 ± 0.11	-0.19 ± 0.07

^a Percentage of nests which raised at least one nestling to fledging age (40-48 days old).

^b Variable fitted to the multivariate models of Table 1.

^c Percentage of nests which had a balcony within a 20 m radius.

^d Percentage of locations with poor sanitation.

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

Nishant Kumar, Urvi Gupta, Harsha Malhotra, Yadvendradev Jhala, Qamar Qureshi, Andrew Gosler
& Fabrizio Sergio

Abstract

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 thus 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. Similarities 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.

Keywords: human culture; human subsidies; nest availability; population limitation; tree management; urban raptor

Research



Cite this article: Kumar N, Gupta U, Malhotra H, Jhala YV, Qureshi Q, Gosler AG, Sergio F.

2019 The population density of an urban raptor is inextricably tied to human cultural practices. *Proc. R. Soc. B* **286**: 20182932.

<http://dx.doi.org/10.1098/rspb.2018.2932>

Received: 27 December 2018

Accepted: 14 March 2019

Subject Category:

Global change and conservation

Subject Areas:

ecology

Keywords:

human culture, ecosystem services, human subsidies, nest availability, population limitation, tree management

Author for correspondence:

Nishant Kumar

e-mail: nishant.kumar@zoo.ox.ac.uk

[†]These authors contributed equally.

^{*}Present Address: Ashoka Trust for Research in Ecology and the Environment, Royal Enclave, Srirampura, Jakkur, Bengaluru, Karnataka 560064, India.

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4442987>.

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

Nishant Kumar^{1,2}, Urvi Gupta^{2,†}, Harsha Malhotra^{2,†,‡}, Yadvendradev V. Jhala², Qamar Qureshi², Andrew G. Gosler^{1,3} and Fabrizio Sergio⁴

¹Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

²Wildlife Institute of India, Post Box no. 18, Chandrabani, Dehradun, Uttarakhand 248001, India

³Institute of Human Sciences, School of Anthropology and Museum Ethnography, 58a Banbury Road, Oxford OX2 6QS, UK

⁴Department of Conservation Biology, Estacion Biologica de Doñana-CSIC, C/ Americo Vespucio 26, 41092 Sevilla, Spain

NK, 0000-0002-3505-6800; YVJ, 0000-0003-3276-1384

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



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 km² 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 km². These were plotted randomly within Delhi (1500 km²) 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

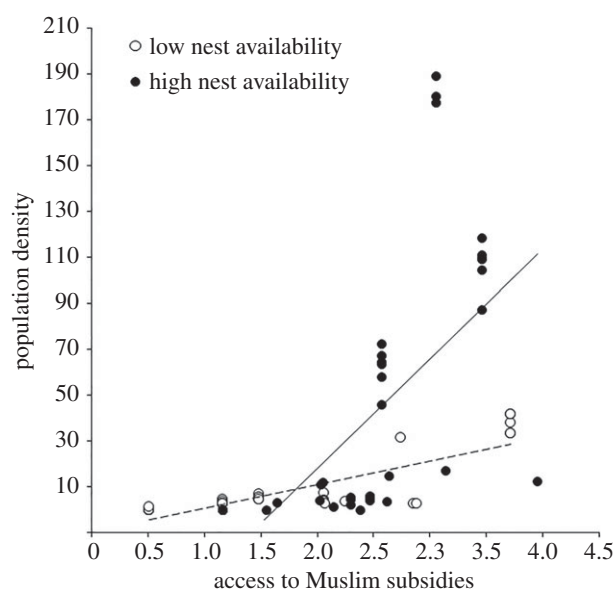


Figure 2. The population density of black kites in the megacity of Delhi (India) increases with food availability (access to Muslim subsidies), but such a relationship is modulated by the availability of breeding sites. For clarity of visualization, nest availability is here depicted as high (above the 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	$B \pm \text{s.e.}$	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, Dehradun (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.

Funding. This work was supported by the Raptor Research and Conservation Foundation (Mumbai), by the Government of India, Ministry of Environment, Forest and Climate Change and by project CGL2015-69445-P of the Spanish Ministry of Economy and Competitiveness with Feder Funds to F.S. N.K. was funded by the Felix Scholarship Trust and Sumerville College, Oxford University.

Acknowledgements. We thank Dr L. Kruuk, S. Barrett, Dr W. Cresswell, A. Tanferna and an anonymous associate editor and reviewer for constructive comments on an earlier draft of the manuscript, and Ujjwal Kumar and the Director, Dean and Research Coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. Delhi Police, and the Forest Departments of Delhi and Uttar Pradesh, Delhi Transport Corporation, civic bodies of the Government of NCT of Delhi helped with legal permits, and the Director of the National Zoological Park of New Delhi gave access to study kites in the Park. Miranda House College and University of Delhi allowed access to their campus for nest monitoring. We thank Laxmi Narayan, Prince Kumar, Poonam and all the members of the ‘Black Kite Project Group’ for help in the field, especially A. Singh, P. Kumar, H. Singh, U. Nair and M. Singh.

References

- United Nations. 2014 *World urbanization prospects: the 2014 revision highlights*. New York, NY: United Nations.
- Malakoff D, Wigginton NS, Fahrenkamp J, Wible B. 2016 Rise of the urban planet. *Science* (doi:10.1126/science.aaf5729)
- 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.
- Gaston KJ (ed.) 2010 *Urban ecology*. Cambridge, UK: Cambridge University Press.
- Niemelä J (ed.) 2011 *Urban ecology: patterns, processes and applications*. Oxford, UK: Oxford University Press.
- 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)
- 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)
- 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, Zumbunnen 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, Warren 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.0204549)
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 Sainly 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, Donazar 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, Taylor 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)

Table S1. Landscape and human variables used to characterize each study plot in which we surveyed the population density of Black kite breeding pairs within the city of Delhi (India). Variables were 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 (Kumar et al. 2018a,b, 2019). These variables characterized each plot in terms of its landscape structure, food availability (local availability of organic garbage, access to Muslim ritual-subsidies, local density of humans walking in the streets), and nest-site availability. See the Study Area section for background details on the rationale underlying the choice of indicators of human refuse and ritual subsidies.

Variable	Description
Nest-site availability	Density (number/km ²) of structures potentially capable to support a kite nest, such as trees of sufficient height, or anthropogenic structures such as pylons and towers (Kumar et al. 2018a). For each plot, we: (1) digitized all large-enough trees clearly visible in Google Earth imagery; (2) visited each plot and mapped any additional trees that were not well visible in Google Earth (e.g. because of low quality, blurred imagery for some sectors of Delhi, or because of the shadow produced by tall buildings) and all potential anthropogenic nest-structures (e.g. poles, towers) that were typically too difficult to detect in Google Earth. For plots in which nesting-structures were too many to count individually, we: (1) plotted 20 random locations within each plot; (2) visited them in the field and counted all nesting-structures observed in a circular buffer of 200 m radius centered on each of these 20 random locations to calculate a cumulative density of nesting structures/km ² . 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.
Refuse availability score	Level of sanitation of the plot: 1 = clean areas (efficient waste disposal with very scarce or no organic refuse in the streets); 2 = areas under poor waste management regime (abundant and widespread refuse in the streets throughout the area, either in small frequent piles, in illegal ephemeral dumps, or as individual items scattered a bit of everywhere through all streets).
Human density	Average number of people walking within 2m of a stationary observer during 5 min at 10 locations randomly plotted within 200 m of a nest, and averaged over all nests censused in a plot. Counts were only operated between 10:00-17:00 hrs and avoided during atypical, momentary peak periods of human traffic, such as exits from work or schools, in order to maintain consistency across sites (following Kumar et al. 2018a).
Access to Muslim subsidies	First component (PC1) of a principal component analysis on the density of Muslim inhabitants in the plot and on the proximity of the plot to the three closest Muslim colonies. A key variable in our previous analyses on the

predictors of kite site selection, occupancy, breeding and behavioral performance was the ease of access to dense Muslim colonies, which provide abundant food supplies in the form of ritual subsidies (Kumar et al. 2018a, b). More specifically, we previously showed that Delhi kites over-selected breeding sites closer than available to the 1st, 2nd and 3rd nearest Muslim colony (see Kumar et al. 2018a for details). Thus, to provide a comprehensive measure that integrated the proximity to the three nearest Muslim colonies with their human population density (under the assumption that higher rates of refuse and ritualized-feeding should occur in more densely-populated Muslim colonies), we extracted the first axis (PC1) of a Principal Component Analysis (PCA) run on these four aforementioned variables. Its PC1 (hereafter “access to Muslim subsidies”) explained 83% of the variance and had a high positive loading on Muslim population density and high negative loadings on the distance to the 1st, 2nd and 3rd closest Muslim colonies. Thus, it provided an increasing index of access to abundant “Muslim subsidies” (details in Kumar et al. 2018a).

Index of road density

Number of asphalted roads crossed by a 500 m north-south and a 500 m east-west transect crossing each other on a nest, and averaged over all nests censused in a plot.

Appendix S1. Spatial analysis of Black kite density

Methods

Because of potential spatial dependency, kite density was initially modelled through a spatial linear mixed model (LMM) by means of Bayesian methods, as detailed in Zuur et al. (2017). The model incorporated a Gaussian Markov random field that controls for spatial dependency and autocorrelation. The estimation of the spatial random field was based on the creation of a dense triangular grid (mesh) overlaid on the study area (Fig. 1 below) to solve a “continuous domain stochastic partial differential equation” (SPDE), in turn used to calculate the parameters of the Matérn correlation function which estimates the spatial random term. The explanatory variables (see Methods and Table S1) were fitted to the model through diffuse priors, and considered as “important” when their 25 % and 95 % credible intervals did not overlap zero. Study plot identity was always fitted as a random effect. Support for inclusion of a spatial random field was examined by comparing the LMM with and without the spatial field by means of the DIC statistic. Zuur et al. (2017) suggest a $\Delta\text{DIC} > 10$ units to provide support for a model over another. All model building and checking procedures follow Zuur et al. (2017).

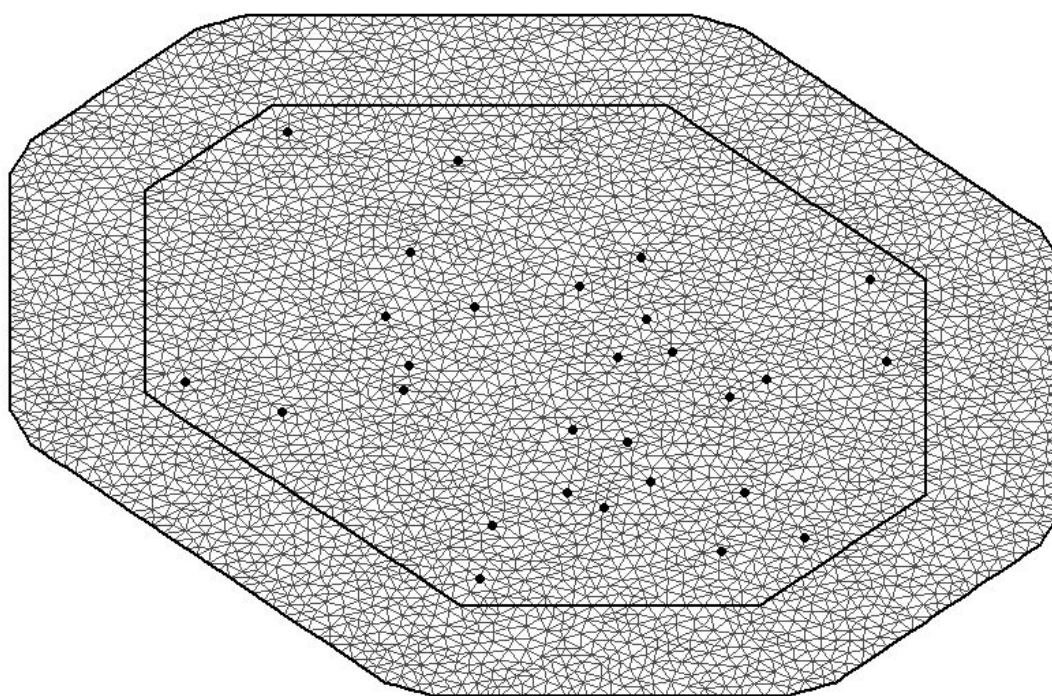


Fig. 1. Mesh overlaid on the Delhi study area to estimate the spatial field fitted to the linear mixed model used to relate kite density to explanatory variables. The mesh was based on a grid of > 4000 triangle-vertices (4299), following recommendations by Zuur et al. (2017). The black circles represent the kite study plots.

Results

Two variables appeared as important, as their 25 % and 95 % credible intervals did not overlap zero (see Table 1 below). These were: human density and the interaction

between Access to Muslim subsidies and Nest availability. There was poor support for the need of a spatial random field: the spatial model was only 2.78 DIC units less than the model without a spatial random field.

Table 1. Slope and credible intervals of a spatial linear mixed model testing the effect of landscape structure, food availability and breeding-site availability on the population density of an urban raptor. Important variables, whose credible intervals do not overlap zero, are highlighted in bold .

Variable	Mean	25 % credible interval	95 % credible interval
Intercept	-15.33	-44.63	14.55
Access to Muslim subsidies	-3.40	-27.08	20.35
Quadratic effect of Access to Muslim subsidies	-6.84	-18.52	4.87
Nest availability	-0.01	-0.04	0.02
Hygiene score	-1.27	-4.53	1.96
Human density	18.18	3.76	32.23
Index of road density	1.04	-1.64	3.76
Access to Muslim subsidies * Hygiene score	0.87	-0.99	2.74
Access to Muslim subsidies * Nest availability	0.01	0.01	0.03

GPS-telemetry unveils the regular high-elevation crossing of the Himalayas by a soaring raptor: implications for definition of a “Central Asian Flyway”

Additional research activities as a background support to Chapter 6

During the development of the thesis, I had occasion to participate to a paper that is directly related to this chapter and which assessed the potential impact of GPS-tagging on Black kites, using data from an intensive tracking-study on the Spanish population. I participated to the statistical analyses of this assessment, as part of my training into radio-tagging afforded by Dr. F. Sergio and his research group, and aimed at familiarizing myself with radio-tagging techniques and GPS-data processing in order to re-apply these techniques to my Delhi study population. The assessment led to a co-authored paper, titled, ***“No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring”***.

Sergio, F., Tavecchia, G., Tanferna, A., López Jiménez, L., Blas, J., De Stephanis, R., Marchant, T.A., Kumar, N. & Hiraldo, F.

Originally published on August 04, 2015; Volume 52, Journal of Applied Ecology

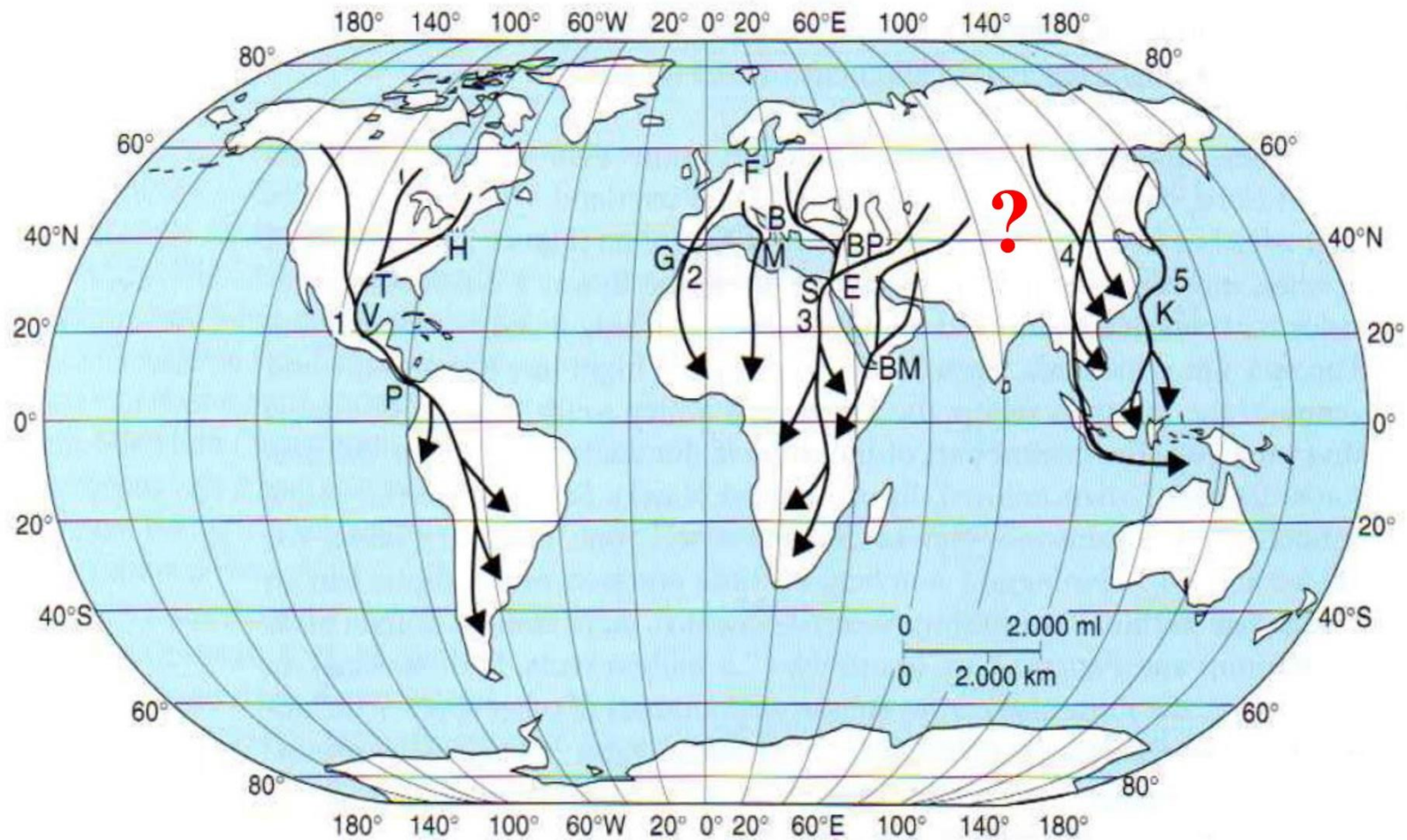
- **Published typesetting included in the Appendix**



Black-eared Kites *milvus migrans lineatus* over the Ghazipur landfill site in Delhi – (Ghaziabad highway) in the peak winter months. About 90% of the flock is constituted by the Black-eared Kites (pers. obs). Photo credit: Dr F Sergio

Abstract

Remote technologies are producing leapfrog advances in identifying migratory routes and the connectivity between breeding and non-breeding areas of migratory species, which are cornerstones to their conservation and management. However, these aspects are still completely unknown for hundreds of common taxa and especially so for Asian migrants, which have received very scanty tracking-research. Here, we used GPS-telemetry to uncover the unknown migration routes and breeding areas of the massive population of migratory Black-eared kites *Milvus migrans lineatus* which winter around the megacity of Delhi, thus contributing to generate the largest raptor concentration of the world. Kites migrated along a rather narrow corridor, almost invariably crossed the Himalaya at extremely high elevations (up to > 6000 m a.s.l.) through its western portion by the K2 of the Karakoram Range and spent large portions of their journey (up to > 500 km) at elevations above 3500 m. They then crossed or circumvented the Taklamakan Desert and the massive Tian Shan Range to reach their previously unknown breeding quarters at the intersection between, Russia, China and Mongolia. Route configuration seemed to respond to the interplay between dominant wind support and barrier avoidance, and negotiation of such major obstacles produced migratory performances comparable to those reported for easier routes. Individual- and population-level wintering ranges were concentrated around Delhi and were smaller than the breeding ranges, likely in response to the massive human waste provided intentionally and unintentionally by an extremely dense human population. Remote-tracking of this extremely common species suggests that high-elevation Himalaya crossing may be more common than previously appreciated. Based on this and previous studies, we suggest the delineation of a hitherto poorly appreciated “Central Asian Flyway”, which must funnel hundreds of thousands of soaring and non-soaring migrants from central Asia into the Indian subcontinent via multiple modes of Himalaya crossing.



Main flyways used by soaring birds globally, according to the recent major review by Newton (2008: page 165). The red question mark highlights the current absence of knowledge which characterizes the flyways for the central portion of the Asian continent. The lower level of knowledge that characterizes the Asian-Australasian migration system was also identified by Newton in his comprehensive review (Newton 2008: page 725).



OPEN

GPS-telemetry unveils the regular high-elevation crossing of the Himalayas by a migratory raptor: implications for definition of a “Central Asian Flyway”

Nishant Kumar^{1,2,3✉}, Urvi Gupta³, Yadvendradev V. Jhala³, Qamar Qureshi³, Andrew G. Gosler^{1,2,4} & Fabrizio Sergio⁵

Remote technologies are producing leapfrog advances in identifying the routes and connectivity of migratory species, which are still unknown for hundreds of taxa, especially Asian ones. Here, we used GPS-telemetry to uncover the migration routes and breeding areas of the massive population of migratory Black-eared kites wintering around the megacity of Delhi-India, which hosts the largest raptor concentration of the world. Kites migrated for 3300–4800 km along a narrow corridor, crossing the Himalayas at extremely high elevations (up to > 6500 m a.s.l.) by the K2 of the Karakoram Range and travelled long periods at elevations above 3500 m. They then crossed/circumvented the Taklamakan Desert and Tian Shan Range to reach their unknown breeding quarters at the intersection between Kazakhstan, Russia, China and Mongolia. Route configuration seemed to be shaped by dominant wind support and barrier avoidance. Wintering ranges were smaller than breeding ranges and concentrated around Delhi, likely in response to massive human food-subsidies. Our results illustrate that high-elevation crossings by soaring migrants may be more common than previously appreciated and suggest the delineation of a hitherto poorly-appreciated “Central Asian Flyway”, which must funnel hundreds of thousands of migrants from central Asia into the Indian subcontinent via multiple modes of the Himalayan crossing.

Identifying migration routes and the connectivity between breeding and non-breeding areas of migratory species is crucial for their conservation, as threats operating during migratory journeys, at stopover sites and in the non-breeding quarters may have marked repercussions on the survival rates of individuals and the persistence of their populations^{1–3}. Remote technologies, such as biologging, are currently providing unprecedented insights into migratory strategies and their population consequences. However, main migration routes are still unknown for most species and over broad geographic areas. In particular, while many remote-tracking studies have focused on species breeding in North America and the western Palearctic, extremely few detailed data exist for species using Asian flyways (e.g.^{4–7}) and most information is still based on route reconstructions hypothesized on the basis of scanty recoveries of ringed birds, or observations at sites that concentrate passing migrants (e.g.^{8–10}). Information on Asian flyways is additionally important because hundreds of species which breed in central-northern Asia spend their non-breeding season in the Indian sub-continent and tropical countries of south-eastern Asia, all of which are experiencing rapid anthropogenic habitat loss and urbanization^{11,12}. This will likely affect the population health of migrants and their potential to spread infectious diseases dangerous for humans, such as avian influenza^{13,14}, particularly in the case of species that are urban human commensals and thus in constant

¹Edward Grey Institute of Field Ornithology, University of Oxford, Zoology Research and Administration Building, 11a Mansfield Road, Oxford OX1 3SZ, UK. ²Mansfield College, University of Oxford, Mansfield Road, Oxford OX1 3TF, UK. ³Wildlife Institute of India, Post Box # 18, Chandrabani, Dehradun, Uttarakhand 248001, India. ⁴Institute of Human Sciences, School of Anthropology and Museum Ethnography, 58a Banbury Rd., Oxford OX2 6QS, UK. ⁵Department of Conservation Biology, Estacion Biologica de Doñana - CSIC, C/Americo Vespucio, 26, 41092 Sevilla, Spain. ✉email: nishant.kumar@zoo.ox.ac.uk

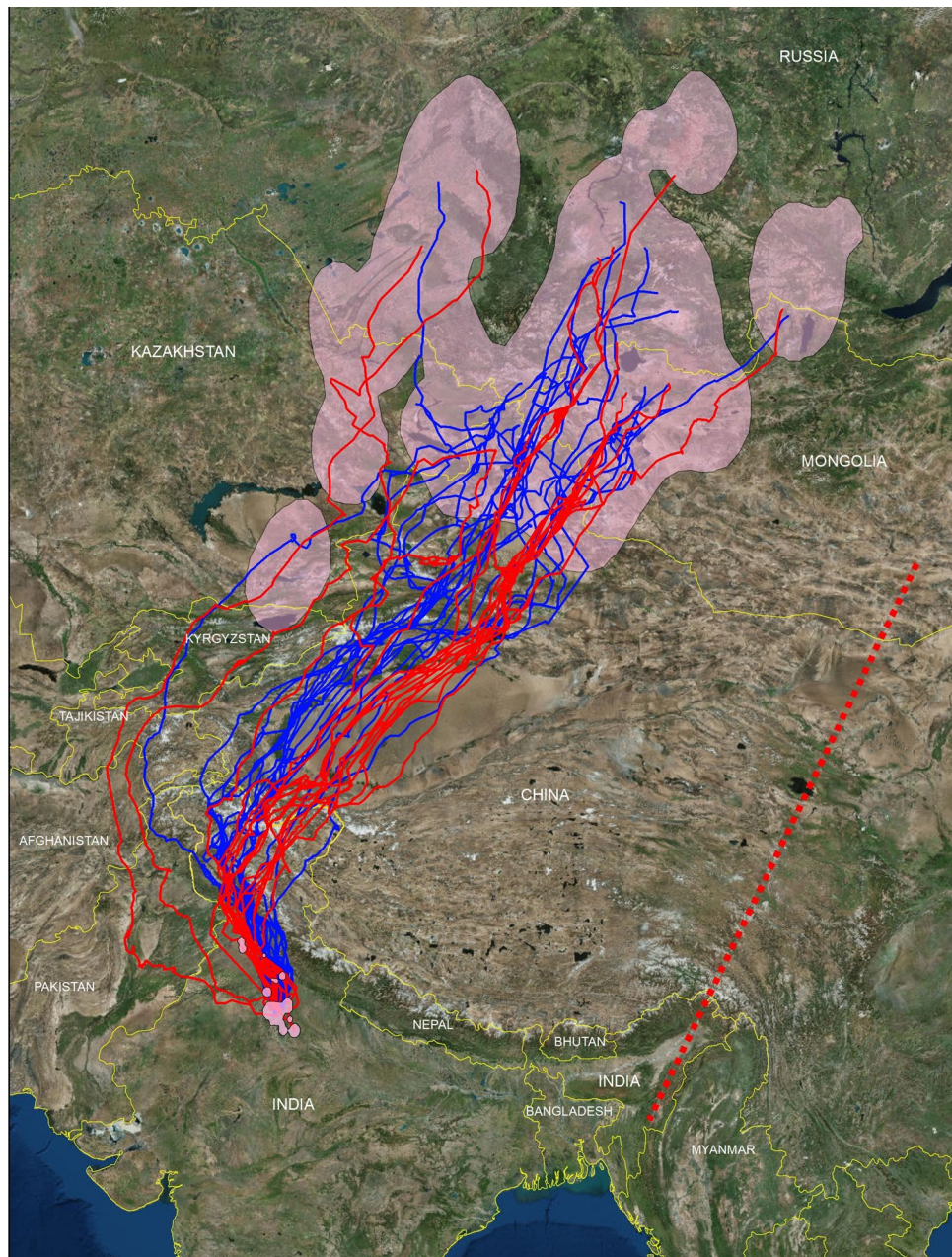


Figure 1. Pre-breeding (blue tracks) and post-breeding (red tracks) migration routes, and breeding and non-breeding ranges (pink polygons) of Black-eared kites *Milvus migrans lineatus* GPS-tagged in Delhi (India). The polygons of the ranges represent 99% Kernels built on the cumulative sum of the GPS-locations of all tagged individuals. The broken red line connects the likely breeding and wintering locations of a *lineatus* kite, based on a ring recovery in North-East India, bordering Myanmar²¹. This map was generated with ArcGIS 10.5, using World Imagery by Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN and the GIS User Community (https://services.arcgis.com/ArcGIS/rest/services/World_Imagery/MapServer), and country borders according to Google Earth imagery (Google India).

close contact with dense human populations. Thus, delineating the migration routes of such human commensals entails additional urgency.

Finally, one of the least known aspects of the Asian migration system is how soaring migrants travelling to and from the Indian subcontinent cope with the major obstacle represented by the Himalayan range. While recent studies have extensively uncovered the barrier-passage routes of birds that migrate mainly by flapping flight, such as ducks and geese (e.g. ^{5,7,15,16}), detailed GPS-tracking data for soaring migrants are still almost non-existent, except for a study on a single Steppe eagle *Aquila nipalensis* individual⁶.

Here, we focus on a raptorial human commensal, the Black kite *Milvus migrans*, and illustrate for the first time the migration routes, breeding and non-breeding ranges of the population that winters within and around the

Migration component	N ^a	Pre-breeding migration Mean ± SE (range)	N ^a	Post-breeding migration Mean ± SE (range)	t	P
Departure date ^b	20 (16)	104.15 ± 11.57 (75–126)	17 (14)	243.65 ± 21.78 (224–258)		
Arrival date ^b	20 (16)	126.25 ± 8.12 (97–155)	17 (14)	270.29 ± 40.43 (255–290)		
Speed (km/day)	17 (14)	198.98 ± 14.82 (77.02–267.89)	14 (12)	151.00 ± 12.56 (71.36–253.91)	2.41	0.023
Active speed (km/travelling day)	17 (14)	236.59 ± 7.99 (182.99–302.42)	14 (12)	198.52 ± 8.34 (155.14–276.99)	3.28	0.003
Duration (days)	17 (14)	22.82 ± 2.67 (13–45)	14 (12)	27.14 ± 2.88 (12–47)	1.08	0.281
Travelling days	17 (14)	17.00 ± 0.94 (13–25)	14 (12)	19.00 ± 1.33 (11–27)	1.26	0.218
Number of stopovers	17 (14)	1.65 ± 0.34 (0–5)	14 (12)	2.64 ± 0.41 (0–5)	1.88	0.071
Days of stopover	17 (14)	5.82 ± 2.03 (0–28)	14 (12)	8.14 ± 1.98 (0–28)	0.81	0.426
Route length (km)	17 (14)	3926.56 ± 108.37 (3333.1–4620.5)	14 (12)	3668.18 ± 151.68 (2963.71–4767.74)	1.42	0.167

Table 1. Estimates of pre-breeding and post-breeding migration by Black-eared kites GPS-tagged in Delhi during 2014–2018. ^aNumber of migration episodes (number of tagged individuals). ^bJulian date (1 = 1 January). Differences in mean values were tested by means of a t-test and significant results are highlighted in bold.

city of Delhi (India), thus contributing to generate the largest raptor concentration of the world^{17–19}. The Indian subcontinent hosts two main Black kite subspecies: *M. m. govinda* or Small Indian kite, which is a resident or semi-resident breeder nesting almost exclusively in urban settings, and *M. m. lineatus* or Black-eared kite, which is a migratory visitor from its northern breeding areas in central-northern Asia^{20,21}. The exact provenance and migration routes of the *lineatus* individuals that spend their non-breeding months in India are virtually unknown, except for a single ring-recovery at the end of October 2001 in North-eastern India (at the border with Myanmar; 24.36°N, 93.54°E), just south of the easternmost Himalayas, of a bird ringed in south-central Mongolia (44.25°N, 105.19°E)²². The current knowledge of the migratory and wintering patterns of *lineatus* kites in India is further muddled by several reports of large winter roosts of Black-eared kites near rubbish dumps or in urban settings misidentified as Small Indian kites, given the complexity of separating the two subspecies, especially when looking at hundreds and sometimes thousands of individuals at once (e.g.^{23,24}).

Results

The migration tracks of all tagged kites are shown in Fig. 1. There was no evidence of kites migrating by night. Pre-breeding and post-breeding migrations largely overlapped: kites crossed the Himalayas in its western portion (Trans-Himalayas), traversed or circumvented the Taklamakan Desert of the Xinjiang Province and the Tian Shan Mountain Range of China, ending up in a wide region centred on the Altai Mountain Range at the intersection of western Kazakhstan, southern-central Russia, western Mongolia and North-western China (Fig. 1). In three cases (one northbound and two southbound migrations), kites took an even more westerly route which brought them to the same destination through eastern Pakistan, Afghanistan, Tajikistan and Kyrgyzstan (Fig. 1). Overall, the tagged kites travelled relatively fast, completing a 3300–4800 km journey in 13–47 days, progressing on average by 150–240 km/day, with significantly faster speeds in the pre-breeding migration (Table 1).

The mean area of individual home ranges was larger during the breeding season (57,515 ± 30,151 km²) than in the non-breeding Indian range (195 ± 59 km²; Mann–Whitney U test = 55, P < 0.05). Similarly, the cumulative range of all tagged individuals was 85-fold larger in the breeding quarters (1,520,099 km²) than in the Indian wintering quarters (17,898 km²). In India, all individuals were constantly located in highly anthropogenic habitats, almost invariably in the vicinity of rubbish dumps, abattoirs, slaughterhouses and other animal processing facilities. On the contrary, breeding ranges were mainly located in natural or semi-natural habitats: out of 20 identified breeding ranges by 16 individuals, 13 were dominated by extensive farmland, 5 by arid–steppe habitats and one by marshland (based on inspection of Google Earth imagery). Interestingly, one of the four kites that could be tracked for two consecutive breeding periods (data are still accumulating for the rest) radically changed its range from one year to the next, moving from North-western China to a site some 1100 km away in South-central Russia, which may suggest dependence on ephemeral resources.

Discussion

The GPS-tagged kites accomplished a 3300–4700 km migration that connected their non-breeding quarters around the trapping site in Delhi to a rather compact and continuous breeding range at the intersection between western Kazakhstan, Northern China, western Mongolia and southern Russia. The route was similar between the pre- and post-breeding migrations and ran as a relatively narrow corridor that passed through several important successive macro-barriers, such as the Himalayas, the Taklamakan Desert of southern China and the Tian Shan mountains.

In both northbound and southbound migrations, kites did not cross the Himalayas through the most direct route to-from their breeding grounds, but rather made a detour of 400–1000 km north-west of Delhi to cross the Himalaya barrier between Punjab and Kashmir. A few individuals made an even more western detour through Pakistan and Afghanistan and thus almost completely avoided the extremely high crossings of the Himalayas. However, most kites crossed the Himalayas by the Karakoram mountain range, several of them by its highest K2 peak at extremely high altitudes of up to more than 6500 m a.s.l., as recorded by the on-board GPS and as confirmed by the terrain below. Furthermore, many individuals covered stretches of more than 500 km with

Figure 2. Main Asian flyways (red lines) used by soaring migrants in Asia during pre- and post-breeding journeys. Traditional flyways-charts (e.g.^{2,31}) depicted two major flyways for Asia: the Eurasian—East African flyway (G) and the East Asian Continental flyway (H). We propose the addition of a composite “Central Asian flyway” (routes A to F) employed by soaring migrants from central Asia to enter or exit their non-breeding quarters in the Indian sub-continent. The passage of soaring migrants is likely to be mainly funnelled through the westernmost (A, B and C) and easternmost (D, E and F) ends of the Himalaya Range. The eastern crossing of the Himalayas has been poorly documented by tracking-studies for soaring migrants and thus three hypothetical nonexclusive routes are shown. The connection between route D and E is supported by satellite-tracking data on a single Steppe Eagle by Batbayar and Lee⁶. Plotted routes B and C are based on data from this study, while route A is based on tracking data by Juhant & Bildstein¹⁰ and Terraube and colleagues⁴⁰. Based on terminology proposed in Juhant & Bildstein¹⁰ and new routes outlined in this study, we define: route A and B as the “Western Circum-Himalayan Corridor”; route C as the “Western Himalayan Corridor”; route D and E as the “Eastern Himalayan Corridor”; and route F as the “Eastern Circum-Himalayan Corridor”. The red dashed line represents a West–East migration corridor reported by several authors for several raptors, especially for the autumn migration (western Himalaya⁹; eastern Himalaya^{6,41,42}). It may represent the strategic, approaching movement to the Himalaya crossing in the pre-breeding migration, or the post-crossing exploitation of favourable winds in the post-breeding migration. More tracking data from more species will be needed to uncover its function. The blue dashed line in western Mongolia indicates a likely migratory divide: species passing to the west/east of such divide seem to use the western/eastern Himalayan routes, respectively. This divide also seems to hold for other non-soaring taxa, such as ducks and geese (e.g.^{5,15,16}). The passage of species capable of migrating through more direct flapping flight or through mixed strategies based on both soaring and flapping (e.g. falcons, harriers, Accipiter hawks) may employ a more central, broad-range crossing of the Himalayas (conceptually approximated by continuous blue lines over a portion only of the Himalaya range to avoid map clogging, (e.g.^{7,15}). The thick red arrows at the top of the map (central-northern Russia) represent the theoretical, more northern basin of provenance of migrants travelling through the more southern depicted routes in the outward, post-breeding migration. The map integrates data from the current study, tracking data from other studies (e.g.^{5–7,16,40}), re-sightings of ringed birds (e.g.²²), observations at watch-sites of concentrated passage by migrants (e.g.^{8–10,41,42}) and previous large-scale maps of main flyways for soaring birds^{2,31}. Major routes are shown only up to their main entry-areas into the Indian subcontinent and into Africa. This map was generated with ArcGIS 10.5, using World Imagery by Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN and the GIS User Community (https://services.arcgis.com/ArcGIS/rest/services/World_Imagery/MapServer), and country borders according to Google Earth imagery (Google India).

unavoidably continuous elevations of > 3500 m a.s.l., thus spending long periods at high altitudes. Overall, such crossings must require special physiological adaptations²⁵ and had been mainly documented as a common population strategy for larger species (e.g. large eagles) or for reputedly more powerful fliers and non-soaring migrants such as falcons, ducks and geese (e.g.^{5,15,16}). The western crossing of the Himalayas was thus unlikely to be caused by mere high-elevation avoidance and was probably determined by some interaction between wind-support and minimization of barrier-threats. In Appendix 1 we show the average wind directions for the main months of migration. Two aspects of dominant winds seem important: (1) direct crossing of the Himalayas by the shortest route from Delhi would expose kites to strong south-westerly winds once on the Tibetan Plateau, which would displace them eastwards, thus causing a subsequent unavoidable 1500–2000 km of continuous journey over high-elevation or desert lands to reach the breeding grounds; (2) on the contrary, dominant winds are less strong and more favourably oriented in the western Himalayas—western Taklamakan Desert, and such route allows (2a) the western circumvention of the desert through large patches of irrigated farmland and (2b) the eastern circumvention of the Tian Shan mountains (with peaks > 7000 m high and elevations often > 3500 m). A more quantitative analysis of wind-and barrier-effects will be presented elsewhere.

Negotiation of wind support and geophysical barriers led to migratory speeds comparable or even higher than those reported in other telemetry studies², and for the nominal subspecies migrating along the west European-west African flyway with markedly less dangerous obstacles^{26,27}. Thus, whatever strategies were in place seemed to afford clear advantages as they led to journeys as efficient as those reported for easier routes. Curiously, in the latter Euro-African study, the post-breeding migration was shorter and more rapid than the pre-breeding migration²⁶, while the opposite was evident in the current Asian study. Such difference is congruent with variation in wind conditions between the two flyways: in the west European—west African flyway, strong headwinds and tailwinds respectively characterize the pre-breeding and post-breeding migration, while wind conditions in the Asian flyway are rather similar between autumn and spring. By exclusion, the higher Asian speeds for the northward migration were likely propelled by the urgency to arrive early at the breeding quarters and the fitness benefits that this ensures in kites and other species (e.g.^{26–29}, review in^{2,30}). This comparison underlines how migration dynamics may change radically between different flyway-systems in response to the delicate balance between barrier negotiation and weather support, even within a single species. This suggests caution in generalizations from studies conducted at a single flyway and underscores the need for more research from the very poorly known Asian flyways.

For example, up to date two major flyways have been reported for Asian raptors and other soaring migrants^{2,31} (Fig. 2): a western route leading from central-western Russia and Kazakhstan to eastern Africa (usually called Eurasian-East African flyway) and an eastern route leading from eastern Russia—Japan to south-eastern Asia, Indonesia and Australia (usually called East Asian continental flyway). This leaves out what can be defined as a “Central Asian flyway”, well appreciated for non-soaring migrants such as ducks and geese (e.g.^{5,17}) but not



for the massive number of soaring birds that must cross the Himalayas each year. This flyway is composed of a series of corridors (routes A-F in Fig. 2), that must funnel hundreds of thousands of soaring migrants from Kazakhstan, central-northern Russia, Mongolia and central-northern China into the Indian subcontinent and vice-versa. Soaring migrants are likely to concentrate their crossings at the westernmost and easternmost ends of the Himalayan range and Tibetan plateau, as shown by our data, other satellite data from a single eagle⁶, and casual observations (e.g.²²), while “flapping” migrants may also cross through the central sectors of Nepal^{5,7} (e.g. blue lines in Fig. 2; see also detailed multi-species maps in¹⁵). These entries or exit routes could be defined as the “Western Circum-Himalayan Corridor” (route A and B in Fig. 2); the “Western Himalayan Corridor” (route C); the “Eastern Himalayan Corridor” (route D and E); and the “Eastern Circum-Himalayan Corridor” (route F). Note that the systematic use of the western portion of this central flyway by all our tagged birds would already imply the passage of thousands of Black-eared kites known to winter around the Delhi region alone, in what is probably the greatest raptor concentration of the world. To our knowledge, such massive and funnelled passage at high-elevation was unknown, may be easily representative of the migration dynamics of other soaring species and it may easily have a similar counterpart somewhere in the eastern Himalayas. Finally, the fact that all our tagged kites bred eastward up to western Mongolia and that the few available data for birds migrating from central Mongolia showed a heading towards the easternmost end of the Himalaya range^{16,22} suggest the possibility of a migratory divide in central-western Mongolia for kites and possibly for other species (blue dashed line in Fig. 2). Birds breeding west or east of such divide would be more likely to use the western or eastern Himalaya-crossing of the Central Asian flyway. Similar threshold-divides have been previously reported for other species (e.g.³²).

Migration connected breeding and non-breeding ranges of very different extent. Both at the individual and cumulative population-level, breeding ranges were way larger than the non-breeding, Indian ranges (Fig. 1). This difference was likely caused by the enormous availability of predictable human food subsidies in the Indian landscape. In the Indian quarters, all tagged kites behaved as specialists of anthropogenic resources: they used landfills and abattoirs almost exclusively, and frequented urban or suburban sites of Delhi and surrounding towns and cities (up to 300 km from Delhi), where they often congregated into flocks of thousands of individuals (up to 10,000 counted by us at a regularly monitored single landfill). This was likely promoted by: (1) the enormous availability of human meat waste in an area of extremely high human density (16 million inhabitants in Delhi alone), ranking as the most important meat-producing area of India³³ and coupled with poor sanitation infrastructures to process such refuse; (2) the additional availability of meat waste intentionally offered to kites by workers of abattoirs and animal processing facilities as part of the religious practice of offering a service to all divine creations. These cultural beliefs are integral to the extremely benevolent attitudes of most Indians to wildlife, which probably further favoured an urban lifestyle by kites, as previously demonstrated for the locally-resident Small Indian kite subspecies^{18,19,34}. Thus, the local availability of enormous human food subsidies likely caused the striking concentrations of thousands of individuals, and the small home ranges and restricted distribution of the tagged kites, which spent all winter in Delhi and surrounding towns. This is in stark contrast with the wintering behaviour of the nominate subspecies in the western Palearctic, whose individuals may range nomadically over several African nations in a single winter^{35,36}. It also contrasts with the behaviour of the tagged kites at the breeding quarters, where they ranged over wide areas, avoiding large cities and usually settling in natural or semi-natural habitats with scattered human populations, such as extensive farmland, steppe, arid rangelands, or wetlands. Only five individuals settled in proximity of medium-small towns, but barely ever used them for foraging.

In conclusion, GSM and satellite GPS-telemetry allowed the efficient monitoring of animal movements across nine Asian nations and from sea level up to above 6500 m high elevations, resolving the mystery of the provenance of the massive concentrations of kites observed in the Delhi-region over winter. In this sense, remote bio-logging continues to unveil biological phenomena that were unthinkable of, up until recently. Our results further implied the systematic migratory crossing of the Himalayas at extremely high elevations by thousands of individuals of a species up to now unknown to accomplish such task and not congruent with the type of flight-mode and capabilities previously associated with such undertakings. This markedly broadens the range of species that may be expected to operate similar migratory tactics, an aspect that has received minor attention and clearly deserves more investigation. Finally, the current data imply the existence of hitherto overlooked migration routes likely used by hundreds of thousands of soaring migrants, thus suggesting the necessity of a better appreciation of the “Central Asian flyway” among the current set of major flyways for avian migrants.

Methods

Ethics statement. This research was part of a larger and long-term study on the demography and movement ecology of Black kites in Delhi. We received the permits to conduct the fieldwork from the office of the Additional Principal Chief Conservator of Forests (APCCF), the Government of the National Capital Territory of Delhi under the provisions of the Wildlife Protection Act, 1972 (permit number: CF/LC/105/07/HQ/10504-8). The Training, Research, and Academic Council (TRAC) of the Wildlife Institute of India, Dehradun (WII), gave bioethical approval for the research protocols. We performed all methods in accordance with the relevant guidelines and regulations laid out by TRAC WII with respect to our study animals.

Field procedures and GPS-tagging. We GPS-tagged 19 Black-eared kites (14 adults and five pre-adults) between 2014 and 2018. Kites were trapped at the landfill of Ghazipur in Delhi by means of mist-nets and Bal-chatri traps positioned over carrion baits. Kites were tagged through 25 g GSM-GPRS PTT manufactured by e-obs GMBH (n = 13 individuals) and PTT-100 Solar Argos/GSM/GPS PTTs of 22 g and 25 g manufactured by Microwave Telemetry, Inc. (n = 6). GPS locations had an estimated error of 18 m. Transmitters weighed less than 3% of the body mass and were fitted as backpacks through a Teflon harness with the same method recently used for the nominate subspecies in another study which showed no adverse effects on body condition, foraging per-

formance, breeding output, survival, recruitment and longevity, or on the capability to raise healthy offspring³⁷. Furthermore, the larger size and mass of the *lineatus* subspecies implied that a lighter transmitter-load was imposed in the current study.

Data processing. Given that the duty cycles of the three tag-types varied from 1 GPS-location/hr to over 1000 GPS-locations/day, we down-filtered the data to a uniform sampling interval of one location/hr, so as to obtain estimates comparable to most previous studies and avoid biases caused by pooling data based on differential location sampling regimes³⁸. Migration tracks from tags that showed signs of malfunctioning (e.g. with no locations for consecutive days during migration or for consecutive weeks during the breeding or non-breeding period) were discarded from the analyses. However, if these tags recorded enough locations during the period of migratory departure and arrival, data on migration timing was retained for analysis. For this reason, estimates on departure and arrival dates are based on slightly larger sample sizes.

Migrations were characterized by the parameters commonly used in this type of studies: (1) departure date; (2) arrival date; (3) kilometres travelled per day; (4) kilometres travelled per day of active migration (i.e. a day with more than 50 km of directed flight); (5) number of days to complete the journey (stopovers included); (6) number of travelling days; (7) number of stopovers at staging areas (i.e. a day with less than 50 km of directed flight); (8) number of days of stopover at staging areas; and (9) route length. The spatial extent of the home range of each kite during the breeding and non-breeding period was assessed by means of a 99% Kernel Density estimator³⁹. Two further Kernel polygons were built after pooling the GPS-locations of all individuals, in order to define the cumulative distribution range of the whole population during the breeding and non-breeding period, respectively. To ensure the comparability of such estimates, home ranges were calculated for the two months in which all individuals were simultaneously present, i.e. June + July for the breeding period and November + December for the non-breeding period. Differences between means were tested by means of t-tests for normal data, or Mann–Whitney U tests for data that did not conform to normality. Statistical significance was set at $\alpha < 0.05$, and all means are given ± 1 SE. The figures were generated with ArcGIS 10.5, using World Imagery by Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN and the GIS User Community (https://services.arcgisonline.com/ArcGIS/rest/services/World_Imagery/MapServer), and country borders according to Google Earth imagery (Google India).

Data availability

Data will be available on reasonable request from the authors.

Received: 24 April 2020; Accepted: 10 September 2020

Published online: 29 September 2020

References

- Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S. & Holmes, R. T. Links between worlds: unraveling migratory connectivity. *Trends Ecol. Evol.* **17**, 76–83 (2002).
- Newton, I. *The migration ecology of birds* (Elsevier-Academic Press, London, 2008).
- Schaub, M., Kania, W. & Köppen, U. Variation of primary production during winter induces synchrony in survival rates in migratory white storks *Ciconia ciconia*. *J. Anim. Ecol.* **74**, 656–666 (2005).
- Higuchi, H. *et al.* Migration of Honey-buzzards *Pernis apivorus* based on satellite tracking. *Ornithol. Sci.* **4**, 109–115 (2005).
- Takekawa, J. *et al.* Geographic variation in Bar-headed Geese *Anser indicus*: connectivity of wintering areas and breeding grounds across a broad front. *Wildfowl* **59**, 100–123 (2009).
- Batbayar, N. & Lee, H. Steppe eagle migration from Mongolia to India. In *Bird migration across the Himalayas: wetland functioning amidst mountains and glaciers* (eds Prins, H. H. T. & Namgali, T.) 117–127 (Cambridge University Press, Cambridge, 2017).
- Dixon, A., Rahman, L., Sokolov, A. & Sokolov, V. A. Peregrine falcons crossing the ‘roof of the world’. In *Bird migration across the Himalayas: wetland functioning amidst mountains and glaciers* (eds Prins, H. H. & Namgali, T.) 53–67 (Cambridge University Press, Cambridge, 2017).
- Zalles, J. I. & Bildstein, K. L. *Raptor watch: a global directory of raptor migration sites* (Hawk Mountain Sanctuary, Kempton, 2000).
- Den Besten, J. W. Migration of Steppe Eagles *Aquila nipalensis* and other raptors along the Himalayas past Dharamsala, India, in autumn 2001 and spring 2002. *Forktail* **20**, 9–13 (2004).
- Juhant, M. A. & Bildstein, K. L. Raptor migration across and around the Himalayas. In *Bird migration across the Himalayas: wetland functioning amidst mountains and glaciers*, pp 98–116 (eds Prins, H. H. & Namgali, T.) (Cambridge University Press, Cambridge, 2017).
- Clark, N. E., Boakes, E. H., McGowan, P. J. K., Mace, G. M. & Fuller, R. A. Protected areas in South Asia have not prevented habitat loss: a study using historical models of land-use change. *PLoS ONE* **8**, e65298 (2013).
- Malakoff, D., Wigginton, N. S., Fahrenkamp-Uppenbrink, J. & Wible, B. Rise of the urban planet. *Science* **80**, 272 (2016).
- Yasue, M., Feare, C. J., Bennun, L. & Fiedler, W. The epidemiology of H5N1 Avian influenza in wild birds: why we need better ecological data. *Bioscience* **56**, 923–929 (2006).
- Yanjie, Xu., Gong, P., Wielstra, B. & Si, Y. Southward autumn migration of waterfowl facilitates cross-continental transmission of the highly pathogenic avian influenza H5N1 virus. *Sci. Rep.* **6**, 30262 (2016).
- Palm, E. C. *et al.* Mapping migratory flyways in Asia using dynamic Brownian bridge movement models. *Mov. Ecol.* **3**, 3 (2015).
- Parr, N. *et al.* High altitude flights by ruddy shelduck *Tadorna ferruginea* during trans-Himalayan migrations. *J. Avian Biol.* **48**, 1310–1315 (2017).
- Galushin, V. M. A huge urban population of birds of prey in Delhi India. *Ibis (Lond.)* **113**, 522 (1971).
- Kumar, N., Jhala, Y. V., Qureshi, Q., Gosler, A. G. & Sergio, F. Human-attacks by an urban raptor are tied to human subsidies and religious practices. *Sci. Rep.* **9**, 2545 (2019).
- Kumar, N. *et al.* The population density of an urban raptor is inextricably tied to human cultural practices. *Proc. R. Soc. B Biol. Sci.* **286**, 20182932 (2019).
- Naoraji, R. *Birds of prey of the Indian subcontinent* (Christopher Helm, London, 2006).
- Ferguson-Lees, J. & Christie, D. A. *Raptors of the world*. (2001).
- Choudhury, A. Migration of Black-eared Kite or Large Indian Kite *Milvus migrans lineatus* (Gray) from Mongolia to North-Eastern India. *J. Bombay Nat. Hist. Soc.* **102**, 229–230 (2003).

23. Forsman, D. Identification of black-eared kite. *Bird. World* **16**, 56–60 (2003).
24. DeCandido, R., Subedi, T., Siponen, M., Sutasha, K. & Pierce, A. Flight identification of *Milvus migrans lineatus* 'Black-eared' Kite and *Milvus migrans govinda* 'Pariah' Kite in Nepal and Thailand. *Bird. ASIA* **20**, 32–36 (2013).
25. Scott, G. R. Elevated performance: the unique physiology of birds that fly at high altitudes. *J. Exp. Biol.* **214**, 2455 (2011).
26. Sergio, F. *et al.* Individual improvements and selective mortality shape lifelong migratory performance. *Nature* **515**, 410–413 (2014).
27. Sergio, F. *et al.* Migration by breeders and floaters of a long-lived raptor: implications for recruitment and territory quality. *Anim. Behav.* **131**, 59–72 (2017).
28. Panuccio, M., Agostini, N., Mellone, U. & Bogliani, G. Circannual variation in movement patterns of the Black Kite (*Milvus migrans migrans*): a review. *Ethol. Ecol. Evol.* **26**, 1–18 (2014).
29. Kokko, H. Competition for early arrival in migratory birds. *J. Anim. Ecol.* **68**, 940–950 (1999).
30. Sergio, F., Blas, J., Forero, M. G., Donazar, J. A. & Hiraldo, F. Sequential settlement and site dependence in a migratory raptor. *Behav. Ecol.* **18**, 811–821 (2007).
31. Bildstein, K. L. *Migrating raptors of the world: their ecology & conservation* (Cornell University Press, Cornell, 2006).
32. Flack, A. *et al.* Costs of migratory decisions: a comparison across eight white stork populations. *Science Advances* **2**, e1500931 (2016).
33. Board, C. P. C. *Solid waste management in slaughterhouses* (Ministry of Environment and Forests, Government of India, 2004).
34. Kumar, N. *et al.* 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 (2018).
35. Meyburg, B.-U. & Meyburg, C. GPS-Satelliten-Telemetrie bei einem adulten Schwarzmilan (*Milvus migrans*): Aufenthaltsraum während der Brutzeit, Zug und Überwinterung. *Popul. Greifvogel und Eulenarten* **6**, 311–352 (2009).
36. Blanco, G. *et al.* Integrating population connectivity into pollution assessment: overwintering mixing reveals flame retardant contamination in breeding areas in a migratory raptor. *Environ. Res.* **166**, 553–561 (2018).
37. Sergio, F. *et al.* No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. *J. Appl. Ecol.* **52**, 1665–1675 (2015).
38. Tanferna, A., López-Jiménez, L., Blas, J., Hiraldo, F. & Sergio, F. Different location sampling frequencies by satellite tags yield different estimates of migration performance: pooling data requires a common protocol (migration estimates by satellite tracking). *PLoS ONE* **7**, e49659 (2012).
39. Seaman, D. E. & Powell, R. A. An evaluation of the accuracy of Kernel density estimators for home range analysis. *Ecology* **77**, 2075–2085 (1996).
40. Terraube, J. *et al.* Broad wintering range and intercontinental migratory divide within a core population of the near-threatened pallid harrier. *Divers. Distrib.* **18**, 401–409 (2012).
41. DeCandido, R., Gurung, S., Subedi, T. & Allen, D. The east–west migration of Steppe Eagle *Aquila nipalensis* and other raptors in Nepal and India. *Bird ASIA* **19**, 18–25 (2013).
42. Subedi, T. R. *et al.* Population structure and annual migration pattern of Steppe Eagles at Thoolakharka Watch Site, Nepal, 2012–2014. *J. Raptor Res.* **51**, 165–171 (2017).

Acknowledgements

We are grateful to Dr. F. Lei, Dr. U. Mellone and an anonymous reviewer for constructive comments on a previous draft of the manuscript. We thank Ujjwal Kumar, Alessandro Tanferna, Rachel Godinho, Anoushka Kumar, Ketan Joshi, Chinmay Agarwal, Abhimanyu Bhardwaj, Yukti Taneja, and the Director, Dean and Research Coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. We thank Laxmi Narayan, Prince Kumar, Poonam and all the members of the “Black Kite Project Group” for help in the field, especially H. Malhotra, P. Justa, A. Singh, P. Kumar and G. Singh. The project was funded by the Raptor Research and Conservation Foundation (Mumbai), Microwave Telemetry Inc. (USA) through the Christiane Howey raising scholar award to N.K., and by the Govt. of India, Ministry of Environment, Forest and Climate Change. N.K. was funded by the Felix Scholarship Trust and Somerville College, Oxford University and F. Sergio by project PGC2018-095860-B-I00 of the Spanish Ministry of Science, Innovation and Universities with Feder Funds.

Author contributions

N.K., U.G., Y.V.J., Q.Q., A.G.G. and F.S. conceived the ideas and designed methodology; N.K., U.G., Y.V.J., Q.Q. and F.S. did the fieldwork and collected the data; N.K. and U.G. curated the data; N.K. and U.G. analysed the data; N.K. and F.S. led the writing of the manuscript; U.G. and N.K. prepared figures. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to N.K.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

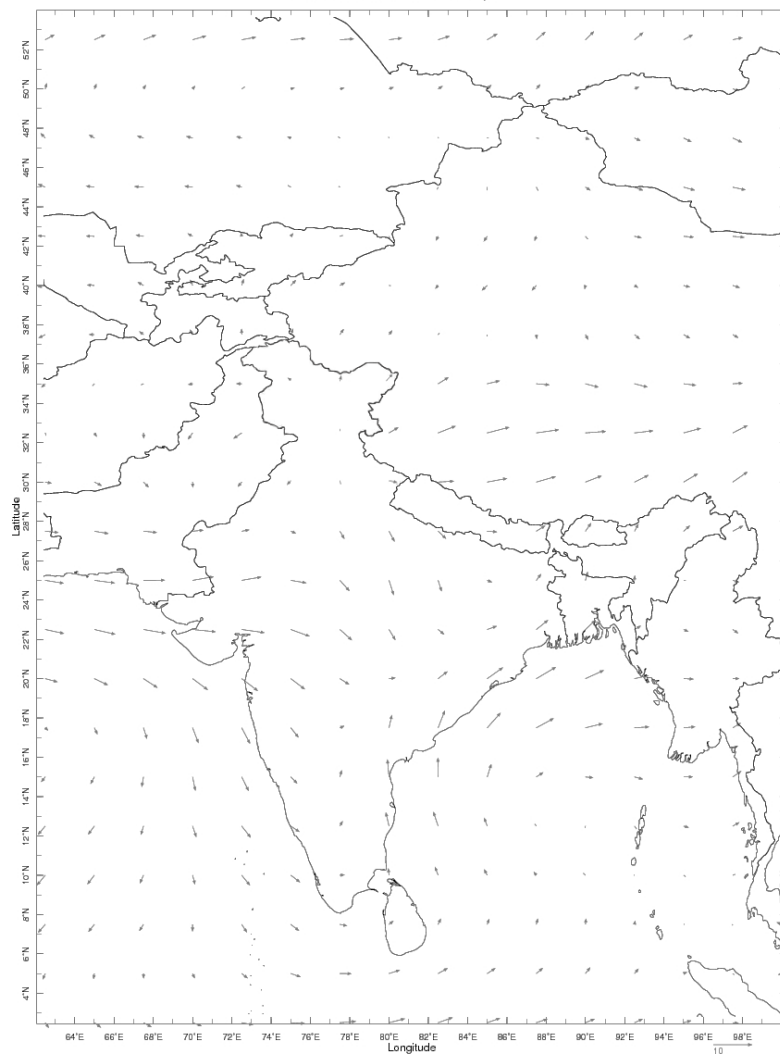


Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2020

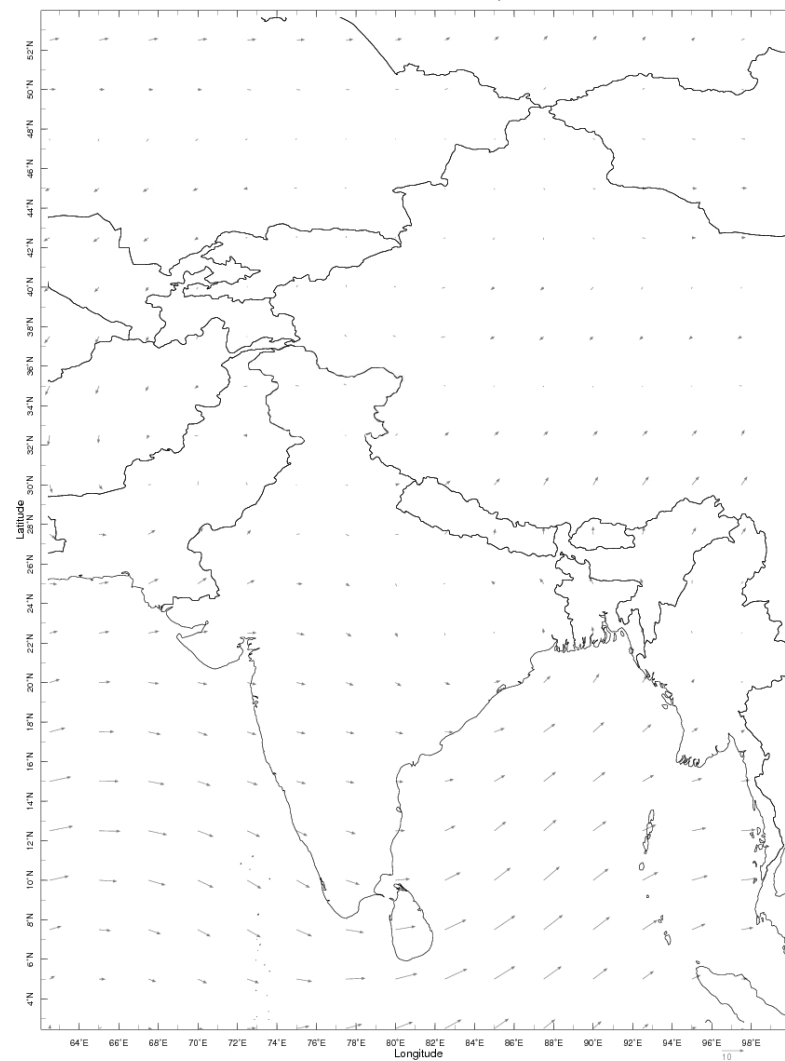
Appendix 1. Dominant winds along the migration route of Black-eared kites wintering in the region of Delhi (India). A: dominant winds in April (the period of peak pre-breeding migration of the GPS-tagged Black-eared kites); B: dominant winds in September (the period of peak post-breeding migration of the GPS-tagged Black-eared Kites). Wind conditions were similar over contiguous months (e.g. May, or October). Except for the Himalaya crossings, Black-eared kites mostly travelled at 700-1500 m elevation. Maps A and B were extracted for an elevation of 762 m a.s.l. Charts from 1500 m elevation showed similar wind dynamics. Arrow lengths are proportional to wind speed. Data downloaded from the NCEP-NCAR Reanalysis of NOAA, based on monthly wind conditions averaged over 1981-2010 (http://iridl.ldeo.columbia.edu/maproom/Global/Climatologies/Vector_Winds.html).

Pressure 925.0 mb Time Apr



A

Pressure 925.0 mb Time Sep



B

This dissertation is part of a larger and long-term study on the demography of Black Kite in Delhi. In the previous chapters, I have shown several ways in which kites have managed, at both the individual and population-level, to adapt to and exploit the urban environment provided by humans, together with its anthropogenic subsidies that offer a potential food bonanza to a facultative scavenger species like the Black Kite. Below, I offer a brief recapitulation of the main results of each chapter, I especially highlight the results that may be of interest to a broad audience rather than to a selected group of kite or raptor enthusiasts, and then proceed to expose the future research directions that will emanate from the results exposed in this thesis.

A cursory examination of the study population in 2013 corroborated and elucidated the previously established importance of extensive and predictable foraging opportunities for an urban population of a facultative scavenger, the Black Kite (Galushin, 1971; Malhotra, 2007). I started my doctoral dissertation after identifying the long-term stability of the breeding density of kites in Delhi since 1960–1970s (Kumar et al., 2014). This represents the highest ever reported breeding density estimate for a raptor of its size (Chapter 1). The availability of food is further complemented by a stable favourable climate which extends the time span for breeding, as reported for other avian populations exploiting urban food super-abundance. Smaller breeding raptors, such as falcons, usually respond by laying a larger clutch, and multiple broods. Urban kites, in comparison, have benefitted from the low density of potential predators in the city (Lin et al., 2015), a general absence of human persecution and a long history of religious tolerance towards living beings, which sustains wildlife and feral animals at extremely high densities within hundreds of South Asian megacities. Furthermore, while kites did not appear to face any conservation concern, recent urban development is causing widespread

removal of mature trees in many sectors of the city (Paul & Nagendra, 2015). Nest site availability is identified as one of the two pillars for raptor biology, the other being food (Newton, 1979). Because Delhi kites mainly nest on trees and use other structures (e.g. pylons or towers) only when trees are in scarce supply, tree availability could limit the kite population in the future, triggering local declines and re-distributions. In Chapter 5, I demonstrate the importance of nest availability at the population level. Thus, the ecological service provided by kites through removal of organic rubbish, the abundance of the species in Delhi, and the current low sanitary levels of the city can be seen as a template that supports the importance of the continued health and existence of this remarkable raptor concentration in such an urban environment. My preliminary work suggested the need for continued monitoring of this population and its urban nesting habitat in future years.

Research gaps on tropical megacities regarding the interplay between a top trophic predator's habitat selection and human socio-economic aspects were addressed in Chapter 2. Here, the research design examined how our model species exploited its supporting highly anthropogenic ecosystem. While modelling breeding habitat selection by a predator and facultative scavenger in a tropical megacity we took into consideration, the spatial associations that tie together human refuse and its prey-fauna, the ritualized feeding of kites (see detailed descriptions of ritualized feeding practices in Chapter 2, 3, 4 and 5), and habitable vegetation patches. The habitat decisions of kites responded in such a way as to optimize the opportunistic uptake of predictable foraging resources tightly enmeshed with human activities. I found that breeders preferred areas with high human density, with poor waste management, with a road configuration that facilitated better access to resources provided by humans and, in particular,

with ready access to Muslim colonies that provided ritual subsidies. Analysis of the relationship between the same variables and breeding success further confirmed the importance of access to human ritual subsidies. Our results stress the importance of human activities, even politics, history, socio-economics and urban planning at multiple spatio-temporal scales (Chapter 2 and 5) when studying the distribution and habitat associations of predatory and scavenging species within highly anthropogenic ecosystems.

After examining the general status, breeding ecology and habitat choices that allowed kites to cope with a highly anthropogenic environment, I investigated some behavioural aspects that may on one hand be adaptive (in terms of offspring defense against enemies) but on the other create potential conflicts with humans. The analyzed behaviour was the defence of eggs and nestlings by parental kites, which showed how kites were able to subtly discriminate how to act in the presence of people feeding them and in the presence of people approaching their nest and thus representing a potential danger. Thus, in Chapter 3, I elucidated the decision of parent birds to indulge in an aggressive response to human intruders. Here, humans (research team) were a surrogate to test variations in parental investment to imminent threats by potential nest predators. The analysis also explored the fitness consequences of investment in aggressive defense by parent birds. I found that the intensity of nest defense was associated with larger broods, it increased with the progression of the breeding season and was once again related to human socio-religious variables that set the scenario of food availability and territory quality for individual kites, thus impinging on their prospects for breeding success, their parental investment and defense motivation.

In Chapter 4, I “zoomed-in” on an aspect of nest defense that may represent a potential challenge and cost for kites’ ability to persist in a city, namely their frequent attacks on humans during nest defense. In this context, I hypothesized once again that the both ecological and human factors, and especially the latter, could enter the dynamics of human-aggression by kites. Results of this analysis showed that the likelihood of attack responded to human activities and practices, such as unhygienic waste management, ritual-feeding of kites, human density, and urban architecture in the nest-surroundings (the presence of a balcony) that increased the frequency with which kites were exposed to humans, thus contributing to lower their fear. While many behavioural studies have suggested an association between aggression and frequent-close exposure to humans to derive food-rewards, few studies have focused on the potential mechanisms that may generate aggression. Surprisingly, while most people living near nesting kite territories acknowledged the risk of attack in any given moment, their attitudes were strikingly sympathetic towards the birds, even by injured people, likely as a result of religious empathy. This “fragile urban amiability” at the human-animal interface was based on two different trade-off decision paths: **first**, originating from the kites’ end as they capitalise on anthropogenic foraging benefits, and **the second** from the people’ end whose accommodative attitude allowed for the proximity of aggressive animals. From the responses of our interviewees, this attitude appeared to be driven by religious reverence and a recognition of the ecosystem service (refuse removal) provided by the aggression-culprits. These results highlight the importance of socio-cultural factors for urban biota and how these may radically differentiate the under-studied cities of developing countries from those of western nations, thus broadening our picture of human-wildlife interactions in urban environments. I believe that similar dynamics will soon be observed in other cities of the developing and developed world,

as rapid sprawling of urban and suburban areas with their associated food-subsidies is likely to increase proximity and exposure of large predators to humans, and vice versa, leading to heightened worldwide conflicts.

Human socio-cultural factors have been recognized as fundamental drivers of urban ecological processes. But their population-effects on urban wildlife are still poorly known. In the Fifth Chapter, I explored the relationship between human cultural aspects and Black Kite population-level densities and find a tight relationship. I argue that these sorts of relationships are likely to be stronger in tropical cities than in the more extensively studied but very different settings of temperate cities. Our models offer explanations for profoundly different niches for urban wildlife. In particular, I examined how kite populations can capitalize on spatial variation in human subsidies, mainly in the form of philanthropic offerings of meat given for religious purposes. I further argue that this tight connection with human culture has generated the largest raptor concentration in the world, with its spatial variations being further modulated by breeding-site availability. This further supports the qualitative arguments presented in Chapter 1 on the importance of breeding site availability for population limitation. As the limiting factor for urban ecosystems, the availability of trees constrained the level of resource-tracking by the kites and their potential to provide an ‘ecosystem service’. I thus proposed to employ tree management as a potential tool to manipulate kite density (e.g. in the case of aggressive human-kite interactions). A major implication of these results is in managing many urban animals whose key resources are inextricably linked with human culture.

Furthermore, exploration of the possible future scenarios pertaining to the aggressive human-kite interface seems necessary in the context of a rapidly expanding megacity. Understanding such conflicts in detail requires an interdisciplinary approach, combining ecology, ethology and the social sciences, beyond the current scope of this thesis. In addition, it will also need an approach spanning multiple scales of analysis, examining relations that are manifested locally at a nest/breeding territory scale, to the ones that pan out at a landscape level. Drawing this further from the discussions within Chapters 2, 3 and 4, aggressive interactions and boldness to human presence are known to pose a nuisance to humans, moderated by the current cultural geography based on religious reverence for animals. However, quite often, a society's ways to express its identity results in associations with candidate animals, for e.g. dogs and monkeys. This argument could not be timelier, given recent drives to incorporate "smart city" outlooks i.e. modern infrastructure within large tropical cities, and the socio-cultural and political dialogue modulating State and Citizens' expression toward specific 'holy' animals, such as cows, monkeys. In the absence of an active state-based intervention to popularize or celebrate the religio- cultural ties with commensals like kites, the "progressive", younger generations already seem less interested in cultural practices such as ritualized-feeding. I predict that future 'decoupling' of cultural-ecological ties in people and kites would impact in unforeseen ways, much in the line of the Red Kite's fate in the city of London (see below), where progressive improvement of city infrastructure turned kites from 'useful' city scavengers to nuisance animals. In the context of the latter, I also predict the "catalytic effect" of aggressive interactions in humans and kites in the coming decades, towards 'decoupling' of cultural-ecological ties in people and kites. I recommend using anti-bird spikes to deter aggressive kite pairs from nesting very close to a human locality. Such interventions should be coupled with

harnessing the scavenging ecosystem-service of kites in the nearby informal settlements plagued with solid waste issues (see below). These must go hand-in-hand with the Government's periodic attempts to 'improve' and relocate informal settlements, abattoirs, and landfill sites which impact scavengers like kites.

The destruction of informal settlements, as a way of slum "rehabilitation", can disrupt the human-waste-commensal relationship within a local system, forcing the dispersal of co-existing commensals (as aggressive pairs, or as reservoirs and vectors of zoonoses) to surrounding areas, in response to the sudden absence of 'predictable' refuse and ritual subsidies. Data on kite densities, amount and types of waste, and their spatial distribution should be used to test the prediction of higher prevalence of aggressive human kite interactions in the surrounding areas of a slum rehabilitation site. Through the fieldwork, I found that, while food subsidies are a common phenomenon within the city, the inhabitants of affluent 'centres' tend to dislike the constant presence of animals, excreta, or their aggressive behaviour. Following this doctoral research, I explain below, the use of observational, ethnographic and instrumentation aspects which can enhance extensions of this research in monitoring slums rehabilitation and relocation/culling of 'problematic' commensals e.g. kites, monkeys and dogs. Incorporation of empirical and site-specific urban ecological models in estimating the conflict threats by a particular commensal will help to minimize conflict and promote the ecosystem services such animals offer in developing megacities. This thesis proposes indicative mechanisms, whose extension in the form of long term studies on commensals shall aid in opting socially and scientifically informed steps to control, cull or translocate animals.

A comprehensive research project which factored the constituency of human refuse in the diet of an avian scavenger warrants some light on the outputs of the purported ecosystem services provided by the kites. As outlined in Chapter 4 and 5, I calculated a preliminary rough estimate of the annual ecosystem and sanitary services offered by these city scavengers (as tones of organic waste removed by the cumulative population). Kites' direct ecosystem service can be translated in terms of safe disposal of the organic waste, which could otherwise decay and lead to disease outbreaks. This estimate also has likely implications for public health security, which might be quantified in terms of mitigation of zoonotic threats caused by the competitive release of mammalian scavengers within the city, such as feral and stray dogs and rodents. Markandeya et al. (2008) discussed the effect of the competitive release of feral dogs as an outcome of a catastrophic decline of vultures, an argument which I would fully extend to the ecosystem services of the kites, especially in poverty stricken areas, i.e. the informal settlements which suffer from issues of solid waste management. Elaborating on Chapter 5, the incidence of zoonoses like rabies and leptospirosis could be mitigated by quick "crane-assisted tree plantation" near the areas marred by physical and zoonotic conflicts by the non-avian scavengers. Such trees can be used as nesting substrates/communal sites by the resident and migratory populations of kites. With no prior quantitative records of commensals within local city sub-systems, these interventions also need to factor the changes in animal densities as case studies. However, I also suggest the need to evaluate harnessing of scavenging service by identifying trade-offs between waste-disposal benefits and zoonotic-threats carried by kites themselves to densely-populated areas.

No discussion on kites in India can be complete without studying the mega-flocks of wintering Black-eared kites in Delhi and other Indian megacities. In Chapter 6, I propose that many of the recent and historical reports of large or enormous flocks of kites associated with rubbish dumps were likely misidentified as kites of the *M. m. govinda* subspecies. In reality, the Indian subcontinent is an important wintering area for kites of the *M. m. lineatus* subspecies (Black-eared Kite), which breeds in central Asia and uses a network of Indian cities to overwinter. While the fact that Black-eared kites are migrants from central-northern Asia was already known and hypothesized, the frequent difficulty of quickly separating the two subspecies, which extensively overlap in the winter, has muddled knowledge about the extent of its contribution to the enormous kite concentrations observed in cities like Delhi. Furthermore, the migration routes and exact breeding ranges of these Delhi migrants were completely unknown up to now. Thus, to fill this gap of knowledge, I GPS-tagged 19 Black-eared kites and remotely followed their meanderings. The GPS-data showed that the individual and population-level ranges during winter were significantly smaller than the summering ranges, likely due to the massive availability of food, intentionally and unintentionally generated by human subsidies in the Delhi region. As urban and peri-urban landscapes also feature as wintering destinations for waterfowl and several other human commensals, telemetry research on common species such as kites highlights the importance of studies on the species using the Central Asian flyway, and its effect on urban residency and foraging.

Limitations

Possible Methodological Limitations

As explained in the discussion-section of Chapter 1, the reported frequency of the food remains collected inside and under the nest was strongly dominated by scavenged meat scraps, both by mass and number. We did consider this as a cursory assessment. To address the possibility of biases in the cursory approaches to diet analysis, we started deploying trail cameras at nests selected at random, within as many plots as possible. This methodological intervention of following breeding events at 40 nests through 2015-2018 found significant increase in the estimated frequency of scavenged meat scraps delivered by the parent kites (Chapter 5). Further, we aim to monitor about 25 nests every year using camera-trapping devices (model Reconyx Hyperfire), covering again the whole urbanization gradient and including most of the nests which are simultaneously and repeatedly sampled to assess the nestlings' growth rates. It should also be noted that an urban research system severely limits the opportunities of camera placement at a nest, because of the risk of theft of expensive equipment, and local concerns about surveillance. Furthermore, many nests do not have accessible branches to fix the camera, and in Delhi we are not in a position to use power tools as the latter attracts undue attention. Even data collected by a 24 X 7 camera installation at a large number of nests would still carry a bias in terms of the meat brought by the parent birds which never reaches the nest and is consumed by the either, out of the nest. To address this bias in light of estimating the "scavenging ecosystem service by kites", I will be using the tri-axial accelerometry data of modern GPS Platform terminal transmitters (see below). Given that the typical, perched style of feeding by a raptor will be quickly captured by the accelerometry data, I aim to calibrate these instances of foraging by parents away from the nest, to largely address the "holes" of

scavenging ecosystem service not captured by the trail cameras. This calibration can easily differentiate whether or not a parent bird is feeding on a meat chunk/whole bodied prey. Alongside, I also intend to do ground-truth of the tri-axial accelerometry data to calibrate the data analysis software for specific foraging events.

Possible Logistic Limitations in estimates of population numbers and stability of breeding density

On the hindsight, I would stress on the discussion of population numbers and stability of breeding density of kites over the five decades of observation. In chapters 1, 2 and 5, I reported the comparison of only landscape-based estimates of kite density within the capital with the estimates provided by previous studies, all of them conducted in the 1970s. These previous studies(e.g. Galuhin 1971), unfortunately, were not reported with sufficient detail to enable a quantitative comparison, except the reports of number of nesting territories within the National Zoological Park (Chapter 1) by Malhotra (2007). Therefore, my inferences about the stability in density (Chapter 1 and 5) should be taken with caution. Furthermore, the preliminary rationale of establishing the Black Kite Project was to understand the impact of the local loss of vultures on the breeding density of kites. Although I found no significant change in the density estimates, using it as plain-speak “stability in density” over the five decades might be misleading, given the high variance around the mean that I found (Chapter 1). These values should rather be interpreted as qualitative proof of the opportunistic resilience of kites within an urban system, city scavengers which keenly-target foraging resources linked to human activities, politics, history, socio-economics and urban planning at multiple spatio-temporal scales. Finally, continued monitoring of the population in the decades to come will give us the unique opportunity to see how the population of this predator will respond to the future changes

that will surely affect a rapidly modernizing, expanding and ever-evolving megacity such as Delhi.

Conclusion

Over the long-term, Delhi and other rapidly-developing tropical megacities are likely to repeat the past and current development trajectories of western megacities like London (Grossman & Hamlet, 1964). Their rapid socio-economic development in coming decades will largely manifest in terms of changes in internal structure, management and culture, with expectedly marked improvements in sanitary infrastructures and refuse disposal. Like the fate of their congeneric Red Kite *Milvus milvus* in old London, infrastructural developments, economic change, and the already visible cultural shifts in younger generations will imply major alterations in resource availability and predictability for many synurbic species (Francis & Chadwick, 2012; Hulme-Beaman et al., 2016). Such unique systems of human-animal coexistence and its impeding conundrums caused by modernization will bring formidable challenges to urban societies. The results of this thesis suggest that, after centuries of urban colonization and of co-existence by kites with humans, their ecology and behaviour is finely tuned on spatial variation in human religion, hygiene and poverty. Further research is needed on synurbic animals in their mature stage of adaptation to an urban life, to understand the fine-grained adjustments to urban structure and human culture, and to model the up-scaling of individual processes to population-level patterns.

Setting a long-term vision

Over the six years of monitoring at 28 independent sampling plots (complemented by longitudinal monitoring of a subset of 11 plots), I have completed a preliminary data collection of multiple behavioural, life history, and population parameters (e.g. clutch size, brood reduction, nestlings' growth) of the kites, collected all along the urban gradients of Delhi. Time has prevented inclusion of all the collected material into the current thesis, and I have preferred to examine in detail some aspects that particularly fascinated me (e.g. human attacks, relation with human cultural subsidies, migration) leaving so many other, equally interesting aspects for future investigation.

These will receive proper attention in due time, as I plan to continue my (hopefully long) research career developing several further subject that will allow me to disentangle the many facets that compose the overall picture of how kites manage to respond, adapt and exploit humans and their anthropogenic main medium, i.e. cities. In brief, main candidates for my future research will be the placement of camera-traps in nests to assess how diet composition and parental provisioning affect the growth rates, health status and stress levels of nestlings, and how all these parameters are in turn affected by urban, ecological and human socio-cultural factors. This will allow me to explore further mechanistic links that may mediate kites' capabilities of exploiting the urban medium.

A further aspect that is dire need of knowledge is the movement ecology of the resident *govinda* kites and how foraging behaviour responds in detail to the complex environment provided by the city and by its system of frequent but short-lasting and ephemeral episodes of ritualized feeding. Obvious questions regarding such aspects include: how far do individual kites travel to exploit ritualized feeding episodes? How do they detect them? Do some

individuals specialize to attend certain places at specific hours so as to capitalize on more predictable feeding events? Do kites nest more densely close to Muslim colonies so as to better locate ritualize feeding episodes through social facilitation (e.g. by observing the sudden departure of close neighbours)? The rapid miniaturization of GPS-devices will soon enough enable us to tag *govinda* kites in efficient manners in order to set-up ad hoc experiments and intensive monitoring to test such ideas.

In conclusion, the material exposed in this thesis is but the start of an intensive study that I set-up and started during my Master studies and that quickly converted into a long-term endeavour. The chapters here presented should thus be considered as an initial assessment, by necessity incomplete, which will be broadened, enriched and refined over the coming years.

References

- Francis, R. A., & Chadwick, M. A. (2012). What makes a species synurbic?. *Applied Geography*, 32(2), 514-521.
- Galushin, V. M. (1971). A huge urban population of birds of prey in Delhi India. *Ibis*, 113(4), 522-522.
- Grossman, M. L., & Hamlet, J. N. (1964). *Birds of prey of the world*. Crown.
- Hulme-Beaman, A., Dobney, K., Cucchi, T., & Searle, J. B. (2016). An ecological and evolutionary framework for commensalism in anthropogenic environments. *Trends in ecology & evolution*, 31(8), 633-645
- Kumar, N., Mohan, D., Jhala, Y. V., 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), 1-8.
- Lin, W. L., Lin, S. M., Lin, J. W., Wang, Y., & Tseng, H. Y. (2015). Breeding performance of Crested Goshawk *Accipiter trivirgatus* in urban and rural environments of Taiwan. *Bird study*, 62(2), 177-184.
- Malhotra, A.K. (2007). Tiger of sky-Pariah Kite, *PhD thesis*, Shilalekh Publishers, Delhi.
- Markandeya, A., Taylor, T., Longo, A., Murty M.N., Murty S., Dhavala K. (2008). Counting the Cost of Vulture Declines – Economic Appraisal of the Benefits of the Gyps Vulture in India. *Ecological Economics*, 67(2), 194-204.
- Newton I. (1979). *Population ecology of raptors*. Poyser, Berkhamsted, UK.
- Paul, S., & Nagendra, H. (2015). Vegetation change and fragmentation in the mega city of Delhi: Mapping 25 years of change. *Applied Geography*, 58, 153-166.

Urban Waste and the Human–Animal Interface in Delhi

NISHANT KUMAR, APARAJITA SINGH, BARBARA HARRISS-WHITE

It is well-documented that urban waste contributes to the economy by creating livelihoods. Less is known, however, about the role of urban waste in producing human–animal ecologies involving livestock and wild birds. Here, four aspects of human–animal relationships in two urban subsystems involving waste as raw material for both stall-fed livestock (focusing on cows) and foragers (focusing on kites) are discussed. These are the roles of waste as feed; complex spatial relationships between animals, humans and their wastes; high densities of animals and humans leading to conflict over waste; and emerging threats of diseases spilling across social and physical barriers between animals and humans mediated by waste, with implications for the health of urbanised living beings.

The Black Kite research was supervised by Yadvendradev Jhala, Qamar Qureshi, Andrew Gosler, and Fabrizio Sergio. The projects were funded by the Raptor Research and Conservation Foundation (Mumbai), the Government of India's Ministry of Environment, Forest and Climate Change, and the University of Oxford (Felix Scholarship Trust and Somerville College). Delhi Police, the Forest Departments of Delhi and Uttar Pradesh, and the municipal corporations and civic bodies of the Government of NCT, Delhi, helped with legal permits. The authors are grateful to all the members of the "Black Kite Project Group," especially Laxmi Narayan, Prince Kumar, Poonam, U Gupta, Y Taneja, A Mehta, H Malhotra, A Sharma, P Kumar, G Singh, and N Kumar. They are also grateful to *EPW*'s reviewers and editors for their constructive criticism.

Nishant Kumar (nishant.kumar@zoo.ox.ac.uk) is Visiting Fellow at the Department of Zoology, University of Oxford, and a Postdoctoral Researcher at the Wildlife Institute of India, Dehradun. Aparajita Singh (aparajita37@gmail.com) is a Master's student at the Tata Institute of Social Science, Hyderabad. Barbara Harriss-White (barbara.harriss-white@area.ox.ac.uk) is Senior Research Fellow, School of Interdisciplinary Area Studies, Professor Emeritus of Development Studies, and Emeritus Fellow of Wolfson College, Oxford University.

In developing tropical countries, rapid urbanisation, often involving in-migration, has created megacities marked by social and economic heterogeneity (UN 2018). Despite the rapid expansion in research on tropical megacities (reviewed in Niemelä et al 2011), four aspects of urban waste have received limited attention.

First, that waste feeds animals. Urban economic expansion is associated with a rise in the per capita consumption of animal products, especially meat and milk (Pica-Ciamarra 2005; Speedy 2003). Demand for milk has transformed India from a state of acute shortage to being the world's leading milk producer (FAO 2009, 2019). This dietary transition has generated livelihoods for livestock owners in cities, many of whom use urban food waste from domestic and commercial sources as animal feed for their backyard cows and other urban livestock (Narayanan 2019). This is a valuable subsidy to dairy owners in cities and towns. In the process, they also ensure the relatively safe disposal of some urban food waste (Salemdeeb et al 2017). Edible waste in roadside garbage dumps provides food for urban livestock, primarily cows, and other urban animals (Kumar et al 2018a).

Second, the production of edible waste and the distribution of urban animals interact in complex ways in the urban space. Waste gatherers living in informal settlements collect, segregate, and recycle the contents of urban garbage piles containing consumption waste from humans mixed with waste from animals (da Silva et al 2005; Harriss-White 2019; Hayami et al 2006). Gatherers routinely work alongside cows, dogs, and pigs, as well as crows and kites. How can these relationships be characterised? The question whether the responses of human and animal scavengers working simultaneously on garbage piles create systematic trans-species relationships—known as guilds—is work in progress (O'Connor 2000). The forms and functions of guilds developing over urban feed and foraging resources affect cultural constructions of animal co-inhabitants among citizens as well as fine-grained behavioural adaptations by animals to the heterogeneous social environments of cities (Kumar et al 2018b).

Third, rapid changes in urban physical structure, modes of garbage creation and disposal, and the scope and range of urban domestic animal rearing have been accompanied by conflicts. Increasing numbers of undomesticated species have adapted to changing urban environments. Termed as opportunistic species in zoology, a subset has seized opportunities, such as nesting and feeding sites, in response to the patronage

practices of people who also contribute edible waste. As a direct and indirect result, kites, dogs, rhesus macaques, rats, and some cattle have proliferated to become “social nuisances” threatening the livelihoods and well-being of urban people, particularly waste gatherers and residents of informal settlements (Baviskar 2011; Kennedy et al 2018).

High population densities of animals and humans lead to conflicting interactions. Waste figures in these cross-species and multispecies conflicts because it supplies food for animals that compete for territory and themselves contribute to waste. The spatial mosaic of human activity in city streets, along with cultural practices of ritual feeding of animals by humans, and the varied standards of management of human and animal waste combine to surface in aggressive and fearful cross-species encounters (Kumar et al 2018a, 2018b, 2019b).

Fourth, progressively tighter human–animal encounters lead to the spillage of diseases across species (called zoonosis) caused by generalist pathogens shared between multiple hosts and sometimes mediated through the impact of waste around which humans and domestic and feral animals meet, for example, rabies, tuberculosis, leishmaniasis, leptospirosis, echinococcosis, and cysticercosis (WHO 2019). India is thought to have the highest burden of zoonotic threats, concentrated in urban villages and unauthorised settlements where human and animal waste is noticeably accumulated and where livestock is reared in damp, cramped environments (Delia Grace et al 2012). However, this role of waste in zoonosis has not yet been much researched for its health effects on tropical urban humans or animals.

Using evidence for Black Kites, researched and monitored since 2012, together with research carried out between 2017 and 2019 on urban cows and commensal animal species in informal human settlements comprised of *jhuggi-jhopdi* and squatter colonies in Delhi, we contribute to the four research gaps by (i) evaluating the role of waste as livestock-feed, (ii) exploring the relationships of humans and animals to complex and differentiated built and social environments, (iii) assessing human–animal conflicts over waste, and (iv) outlining the importance of zoonotic relations mediated through waste.

Methodology

In the last census, the National Capital Territory of Delhi (NCT) had more than 16 million inhabitants and the region was associated with highest per capita production of solid waste in India (CoI 2011). The national capital's growth has engulfed surrounding villages, incorporated informal settlements of immigrants, and extended to satellite towns, creating a continuous urban sprawl, which came under the purview of the NCT in 1992. Delhi also has the largest city-based animal population (GoI 2017), including (i) at least 60,000 cows mostly reared in urban villages and informal settlements, (ii) semi-domestic or feral animals such as stray dogs (estimated at over 1,90,000), and (iii) wild creatures such as Black Kites (about 28,000 resident breeding pairs and 10,000 birds of the migratory *lineatus* race at the Ghazipur landfill alone) and a substantial population of Rhesus Macaques (whose population census is currently being conducted by the Wildlife Institute of India) (Joshi 2019a, 2019b).

From the original insight that sets of cities form systems in terms of interconnected relations of population, economy, and space (Berry 1964), the concept of system has also been found useful to trace complex material and social relations within cities (Fistola and La Rocca 2013; Petit-Boix et al 2017). These intra-city relations have been framed as subsystems by geographers (Rose 1970; Simmons 1981). And, just as ecosystems in cities are now recognised for their unique configurations, so are ecological subsystems, of which urban waste and decomposition form one open component of a larger urban complex. Waste subsystems and their human–animal relations can be explored in Delhi.

Three aspects of Delhi have significant implications for its waste subsystems. First, systems of solid waste disposal in the city create informal livelihoods in manual garbage segregation (closely interacting with opportunistic urban animals) while leaving edible organic refuse available for semi-stallfed cows and feral animal scavengers. Delhi's network of garbage piles of various sizes and contents, its informal human settlements of precariously poor people, and its great range of animal communities are thought to give the capital a representative character in terms of Indian urbanisation. As in the rest of the country, cows have recently become the objects of resurgent religiously and politically motivated veneration. This is adding to material and social pressures at the tight human–animal interface that we discuss below.

Second, human consumption generates subsystems of animal waste. Despite its relatively small size, the NCT ranks among the top regions of the country for the consumption of animal products, reflecting the city's per capita income, which is three times the national average (GoI 2017; MoF 2018). Over and above the supplies from suburban and rural sites and organised milk cooperatives (MoI 2012), in recent decades, the long-established practice of rearing cows in sheds and backyards has expanded in Delhi. Over 90% of the city's livestock is housed in former villages, now included in the NCT, to such an extent that these suburbs have the highest livestock density in the country, and thus a high level of livestock waste (MoI 2012).

Third, even as volumes of general unsegregated waste, animal remains, and excreta have increased, waste spaces are constrained and the lack of suitable new places for garbage disposal generates conflicts of management. Considering the likelihood of further disruptions to animal communities and ecosystem functions, permission for new landfill sites has been denied in ecologically sensitive zones such as the floodplains of the Yamuna and sites in protected urban sanctuaries and green belts (scs Engineers and Abt Associates 2017). In waste management, civic bodies of the capital also experience conflicts of interest and jurisdiction: the Delhi Development Authority, which makes the city's Master Plan every 20 years including spaces for waste; municipal corporations, which are responsible for garbage collection as well as spaces for dumping (Talyan et al 2008); the forest department of the Government of NCT, which is constantly addressing encroachment by unauthorised dumpers of waste, and animal welfare organisations defending the rights of animals. Litigation by animal

welfare activists has resulted in court judgments forcing cattle-rearing to shift to villages on the urban periphery and the decommissioning of abattoirs and dairies on the grounds of animal cruelty. However, the failure to find new sites has meant that all three of Delhi's landfills continue to function more than a decade after court orders for their decommissioning were passed.

Our arguments are based on two Delhi research initiatives on Black Kites, a prominent avian scavenger, opportunistically responding to the food afforded by unsegregated garbage in the city (Kumar et al 2014, 2018a, 2018b, 2019a). In Delhi, such foraging opportunities support a density of Black Kites that is the highest concentration of a raptor recorded in the world. Over the period 2013–19, kite behaviour has been monitored comprehensively at 30 sampling plots of approximately 1 km² representing conditions ranging from semi-natural to extremely built-up (Kumar et al 2014). Modelling individual-level breeding habitat preferences, and testing for their extrapolation to population-level effects, this research has investigated the effects on bird behaviour of urban landscape structure, human population density, and human practices, including those of waste management (Kumar et al 2018b). Then, from 2017 to 2019, preliminary studies were carried out at the same 30 sampling units on the processing of waste, combining economic, sociological, and ecological perspectives. This has generated insights about the ways in which waste supplies food for feral, opportunistic, and domesticated animals, particularly cattle.

Edible Waste in the Feed Subsystem

In Delhi, in the high-density areas we sampled, residents deposit their household or commercial waste directly on roadsides. This attracts rodents and pigeons that are potential prey for animal predators (Kumar et al 2014). Semi-structured interviews with 10 randomly selected local residents in the sample sites (Kumar et al 2018a) about garbage collection from local dumps by the municipal corporations confirmed our direct observations that the types, numbers, and guild structure of commensals foraging on accumulated garbage are systematically and spatially patterned. Older and newer settlements in Delhi differ considerably in their human and animal densities, their waste-generation practices, and their public sanitation and hygiene. At a micro-level, edible refuse consumed by birds is found to be associated with the width of streets, their human traffic, and the density of overhead electric wires that can prevent them from landing on garbage piles (Kumar et al 2018b). Spatial subsystems in which dumped edible waste is gathered for animal rearing or left in situ for foraging are illustrated here, first for cows and second for kites.

In Delhi, a substantial part of livestock keeping is not registered or regulated by the state. Most cows maintained in backyards are of robust, disease-resistant, native stock with lower daily milk yields and shorter and fewer lactation cycles than the high-yielding cross-breeds characteristic of intensive dairying. Their stock is replenished from the surrounding National Capital Region. The slaughter of cattle for meat creates carcass waste that forms a major component of meat currently offered

to kites. Whereas in villages and small towns, dung from milch cattle is used as fuel or manure, in Delhi, it is either left dispersed in the streets or swept into open drains, adding to Delhi's waste. Decomposing dung is a source of harmful pathogens, greenhouse gases, and noxious odour (Chaudhuri 2015; FAO 2009; Sorathiya et al 2014).

Well-established suburban colonies, for example, slums and the older Muslim-dominated neighbourhoods in east Delhi, may have poor sanitation (Dubochet 2019). After waste collectors have retrieved recyclable material that they can sell from the neighbourhood garbage dumps, waste goes to one of Delhi's three landfills. Municipal officials at the landfill offices explained in interviews that each of the three landfills daily receive about 500 five-tonne truckloads of mixed garbage, much of it potentially edible to animals. The largest is at Ghazipur and covers an area of 70 acres, standing 65 metres high, just 7 metres shy of the heights of the Taj Mahal and Qutub Minar. Commissioned in 1984, this landfill is adjacent to Ghazipur Dairy, Delhi's largest cattle abattoir, and to markets for fish and chicken, and fruit and vegetables (Talyan et al 2008). The migratory populations of Black Kites from Central Asia circle and feed around this complex of the landfill, slaughterhouses, and markets.

Despite the abundance of edible waste, trail cameras fixed on nests revealed that ~90% of the diet of breeding kites consisted of ritual offerings (Kumar et al 2019a). Meat thrown to kites, typically outside local mosques to request blessings, comes from cattle viscera or other slaughterhouse offal supplied by meat shops (of which there are relatively high concentrations in Muslim-dominated neighbourhoods) and informal markets. Such expressions of respect and love for animals mediate physical flows and livelihoods not just in offal for kites, but also in waste meat, fruits, and grains for cows, dogs, macaques, and other animals (Gupta 2016).

Waste, Coexistence and Conflicts between Species

In Delhi, many birds, mammals and insects co-produce and co-consume garbage systems in which the usefulness of edible waste varies by composition and site. Places generating food waste most suitable for animal feed are often separated from the urban villages where animals are reared. Meanwhile, roadside garbage tips and municipal garbage sites are common sites for foraging cows owned—but not stall-fed—by urban producers. In fact, the consumption of edible waste by cattle reduces the costs of milk and meat production, since edible waste compensates for the nutrient deficiencies of the low-quality fodder poor urban cattle-keepers can afford (FAO 2019). Many other animals forage. According to one estimate (Kumar et al 2019b), Delhi's kites annually remove about 4,000 tonnes of edible refuse from its streets and landfills.

In the biodiverse eco-subsystems of Delhi, human–animal ritual feeding sites and practices sustain human, wildlife, feral, and semi-domestic animals at unprecedented breeding densities. Their coexistence and conflicts have been poorly studied from socioecological perspectives (Gupta 2016). People's innate love for living creatures, termed biophilia, often takes the form of religious beliefs wherein animals are forms, vehicles,

or messengers of god (Kumar et al 2019a; Pinault 2008; Taneja 2015). Even in conditions where kites are aggressive, both Muslims and Hindus were found to revere kites. Muslims regard them as embodying sacred qualities, given their role of “winged emissaries,” which take flight bearing sins, worries, or prayers-messages symbolised by the meat offered during ritual-feeding. Many Hindus believe that life forms are interconnected to one ultimate god-form and so tolerate nuisance from animal species, considering them holy beings or even solutions to astrological problems. Many Delhi residents are also sympathetic towards aggressive co-inhabiting animals because of empathy derived from animals’ parenting behaviour and from the realisation that urbanisation has destroyed and degraded the natural habitats of wildlife. Urban residents were found to be well aware of the useful “ecosystem services” provided to their neighbourhood by kites and other animals which consume waste (Kumar et al 2019b).

Attacks on humans by defensive nesting kites were associated with places of ritual-feeding of kites, and with the prevalence of piles of edible waste, which make kites bold and fearless; almost inevitable where human and animal populations both exist at high densities (Kumar et al 2019a, 2019b).¹ In this “entangled urbanism” (Srivastava 2014), aerial/arboreal/ground dwelling animal life-forms enable a range of species, with varying capacities for dispersal, either to indulge in conflicts due to competition over limited resources, or to coexist via niche-segregation in systems dominated by humans. Such urban ecological niches raise the probability of zoonotic transfers.

Waste and Disease Threats

Microbiological pathogens are propagated through urban vectors associated with waste sites. Carcasses are one such site. The loss of the keystone species of vultures from the Indian subcontinent has severely altered the urban food webs and dispersion of carcasses, animal remains, and excreta. Whereas livestock carcasses used to form the main food for vultures, now they are inefficiently consumed by urban commensals such as dogs, rats, crows, and kites. Since dogs are understood to be the main source of rabies in humans in India, the considerable increase in their populations in wake of the decline in vultures has heightened the threat of rabies (Dhavalala et al 2008). Politically motivated reverence for cows now discourages sanitation workers who supply cattle-hide traders with skins from taking the sociopolitical risks involved in preparing cattle carcasses, leaving them increasingly for foragers such as dogs.

In megacities like Delhi, the change in inter-species relations from coexistence to aggressive confrontation stems from population-resource dynamics, which raise the probability of zoonotic transfers. Coexisting species need to negotiate trade-offs between foraging benefits and the perception of threats from humans from other animals and inanimate sources (such as power lines and traffic) (Hulme-Beaman et al 2016; Kumar et al 2019b; Lloyd-Smith et al 2005). In the absence of all but preliminary research quantifying animal responses to (i) the effects of habitat destruction on species and ecosystems, and

(ii) urban concentrations of humans and garbage containing feed for animals, questions about physical conflicts and animal-borne disease at the microbial human–animal interface need urgent answers (Ellis 2019; GoI 2016; Lloyd-Smith et al 2009). Rabies, for instance, is a major concern in Delhi, with over 200 dog bites reported in the capital daily (Singh 2017). Disproportionally higher conflicts have been noted in North and East Delhi, the parts of the capital known to have the lowest standards of solid waste management, including those for edible waste (*Hindustan Times* 2015; Lai et al 2005). Delhi also ranks among the top states in India for deaths due to H1N1 swine flu transferred to humans from backyard pigs fed with food-waste; the threat of zoonotic transfers increases at higher population densities. Increasing incidents of bovine tuberculosis are also a concern (GoI 2016). Many other health consequences of the human–animal interface remain poorly researched or unknown (GoI 2016). Although there have been no detailed studies conducted to evaluate livestock losses from rabies in India, dog-bites and consequent transfer of infection have been reported in almost all domesticated species (Dar et al 2014; Tiwari et al 2019).

Feral ecologies have been the subject of a number of state intervention programmes in Delhi and other megacities, including the drive to control rabies by neutering of street or stray dogs (Kumar 2014). Macaques, for example, have been captured and relocated to the outskirts of the city or sanctuaries, largely driven by the conflicts they create when they attack people and raid homes (*Down to Earth* 2015). These go hand-in-hand with the government’s periodic attempts to “improve” and relocate informal settlements, abattoirs, and landfill sites, but with no records on the impacts of these interventions on the spatial and behavioural ecology of many commensal scavengers. When animal populations and human–animal relations are disrupted without consideration for co-inhabiting domestic animals/commensals, the host–pathogen equilibrium in a local subsystem is also likely to be disrupted. Commensals venturing into new areas in response to alterations in the dispersion of human food waste will alter the spatial distribution of zoonotic transfers taking place through physical conflicts mediated by commensal vectors. Hence, current gentrification drives aimed at improving health and hygiene in a city so heterogeneously developed suggest a paradox of heightened zoonotic threats in the environs of the gentrified areas wherever commensals are pushed out into new urban habitats (Lloyd-Smith et al 2005, 2009).

Conclusions

Delhi has a large animal population being nurtured on its edible waste. One subsystem for waste and animals involves Delhi’s kitchen and commercial food waste providing free raw materials for rearing backyard cows. In another subsystem, mixed roadside garbage piles that include edible waste provide extensive foraging opportunities for Delhi’s animals. The combined effects contribute to one of the densest human–animal interfaces in the urban world. Despite this general density, subsystems of animal adaptation to the spatial concentration and dispersion

of edible waste take patterned forms. Micro-level details of the physical environment—for example, the width of streets in which garbage is heaped—mediate access. Opportunistic animals need to negotiate the presence of people, vehicles, and other non-human species. Opportunistic birds also need to negotiate potentially obstructive overhead power lines. In such ways, urban architecture and the perceptions of urban people shape the feeding, breeding, waste-creating, and waste-mediating behaviour of Delhi's animals.

While urban animals are, for the most part, tolerated by human residents, field research noted that younger people are less interested in religious-cultural expressions and practices such as the use of waste meat for the ritual feeding of kites. A decline in tolerance and respect may trigger human–animal conflicts. In addition, when refuse disposal and sanitation are upgraded in technological and organisational terms, humans and animals will need to adapt further to coexist. New ways of thinking about urban animals need encouragement. Meanwhile, in the absence of high standards of waste disposal, avian scavengers such as kites might even be actively encouraged

where potential breeding structures such as trees are close to edible garbage. On the other hand, ecological subsystems involving a range of mammalian scavengers at local garbage dumps and large-scale landfills are ripe conditions for inter- and intra-specific transfers of disease-causing pathogens, for example, pathogenic coliform bacteria, antibiotic-resistant bacteria, and prions (Sobsey et al 2006).

When urban poverty and waste management are predominant urban planning concerns, this focus on human–animal waste subsystems might seem a luxury. Although new research is urgently needed, the zoonosis already known to be mediated by the varied forms of waste co-produced and co-consumed by creatures such as domestic cows, semi-wild macaques and street dogs, and wild kites is a pressing development problem. As urban planners and policymakers grapple with the problems of rapid urbanisation, perhaps the biggest challenge is urban waste, and perhaps the currently most unrecognised challenge of waste involves the changing roles and services of animals cohabiting with humans, who themselves contribute to waste.

NOTE

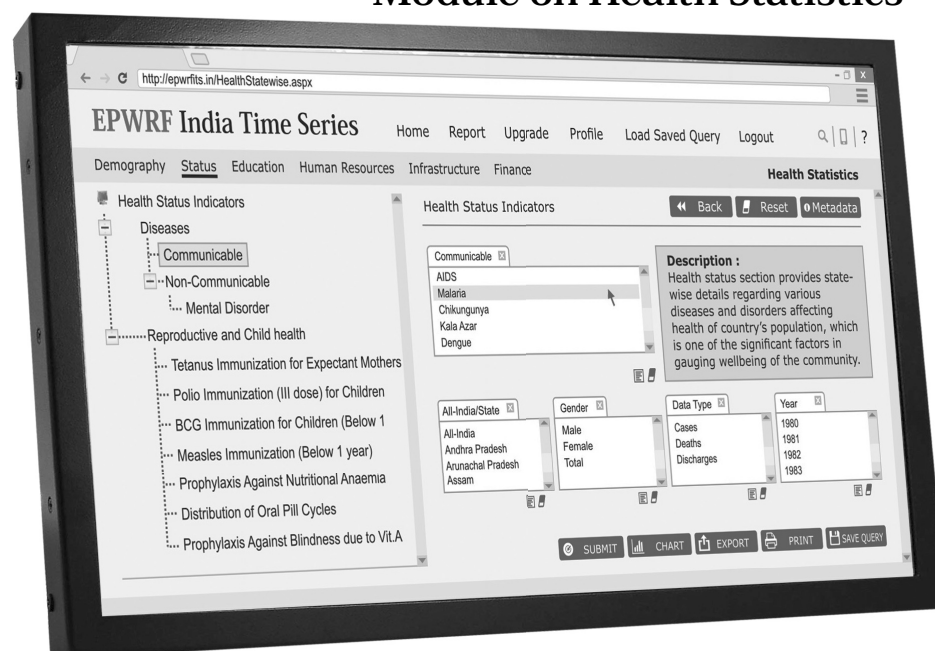
- 1 The study also involved surveys through semi-structured interviews (N=278) to understand the tolerance of and coexistence with birds, and the extent and prevalence of attacks by breeding birds as an act of offspring defence (Kumar et al 2019b).

REFERENCES

- Baviskar, A (2011): "Cows, Cars and Cycle-rickshaws: Bourgeois Environmentalism and the Battle for Delhi's Streets," *Elite and Everyman: The Cultural Politics of the Indian Middle Classes*, Amita Baviskar and Raka Ray (eds), New Delhi: Routledge, pp 391–418.
- Berry, B J (1964): "Cities as Systems Within Systems of Cities," *Papers in Regional Science*, Vol 13, No 1, pp 147–63.
- Chaudhuri, S (2015): "Urban Poor, Economic Opportunities and Sustainable Development through Traditional Knowledge and Practices," *Global Bioethics*, Vol 26, No 2, pp 86–93.
- CoI (2011): "Census of India," Census Organization of India, Government of India, New Delhi, viewed on 22 July 2019, <http://censusindia.gov.in/2011census>.
- da Silva, M C, A G Fassa, C E Siqueira and D Kriebel (2005): "World at Work: Brazilian Ragpickers," *Occupational and Environmental Medicine*, Vol 62, No 10, pp 736–40.
- Dar, K, M Ansari, M Bhat, S Dar and A Hakim (2014): "Studies on Dog Bites of Domestic Animals and Avians in Kashmir Valley," *International Journal of Veterinary Science*, Vol 3, No 3, pp 151–54.
- Delia Grace, F M, P Ochungo, R Kruska, K Jones, I Lapor, M Said, M Herrero and P Duc Phuc (2012): *Mapping of Poverty and Likely Zoonoses Hotspots: Zoonoses Project*, United Kingdom: Department for International Development, UK, https://cgspage.cgiar.org/bitstream/handle/10568/21161/ZooMap_July2012_final.pdf?sequence=4.
- Dhaval, K, A Markandya, T Taylor, A Longo, M Murty and S Murty (2008): "Counting the Costs of Vulture Decline: An Appraisal of Human Health and Other Benefits of Vultures in India," *Ecological Economics*, Vol 67, No 2, pp 194–204.
- Down To Earth (2015): "Relocation of Monkeys in Delhi Good for Everybody," 4 July, viewed on 22 July 2019, <https://www.downtoearth.org.in/news/relocation-of-monkeys-in-delhi-good-for-everybody-5707>.
- Dubochet, L (2019): "Worth the While? Time and Politics in Delhi," PhD thesis, London School of Economics, London, United Kingdom.
- Ellis, E C (2019): "Sharing the Land between Nature and People," *Science*, Vol 364, No 6447, pp 1226–28.
- FAO (2009): "Livestock, Food Security and Poverty Reduction: The State of Food and Agriculture," Food and Agricultural Organisation, viewed on 22 July 2019, <http://www.fao.org/3/i0680e/i0680e03.pdf>.
- (2019): "India: Increasing Demand Challenges the Dairy Sector," viewed on 22 July, <http://www.fao.org/3/i0588e/i0588E05.htm>.
- Fistola, R and R A La Rocca (2013): "Smart City Planning: A Systemic Approach," The 6th Knowledge Cities World Summit, Istanbul, 9–12 September.
- Gol (2016): "Zoonotic Diseases of Public Health Importance: India," Zoonosis Division, National Centre for Disease Control, Government of India, New Delhi.
- (2017): "Husbandry, BAHs-Basic Animal Statistics and Fisheries," Department of Animal Husbandry, Dairying & Fisheries, Ministry of Agriculture, Government of India, New Delhi.
- Gupta, U (2016): "Misplaced Compassion in a Starving Nation," viewed on 22 July 2019, <https://mscbiodiversity.org/2016/12/28/misplaced-compassion-in-a-starving-nation/>.
- Harriss-White, B (2019): "Waste, Social Order, and Physical Disorder in Small-Town India," *Journal of Development Studies*, pp 1–20, doi: 10.1080/00220388.2019.1577386.
- Hayami, Y, A Dikshit and S Mishra (2006): "Waste Pickers and Collectors in Delhi: Poverty and Environment in an Urban Informal Sector," *Journal of Development Studies*, Vol 42, No 1, pp 41–69.
- Hindustan Times (2015): "Over 64k Dog Bite Cases in Delhi, North Delhi Most Affected," 16 December, viewed on 22 July 2019, <https://www.hindustantimes.com/cities/over-64k-dog-bite-cases-in-delhi-north-delhi-most-affected/story-2kgHhZBAYWwpqmyGSvzv6O.html>.
- Hulme-Beaman, A, K Dobney, T Cucchi and J B Searle (2016): "An Ecological and Evolutionary Framework for Commensalism in Anthropogenic Environments," *Trends in Ecology & Evolution*, Vol 31, No 8, pp 633–45.
- Joshi, Hridayesh (2019a): "Monitoring Monkey Business in Delhi," *Mongabay*, 23 October, <https://india.mongabay.com/2019/10/monitoring-monkey-business-in-delhi/>.
- (2019b): "Delhi Government Has a New Strategy to Curb Monkey Attacks: An Area-wise Census," *Scroll.in*, 28 October, <https://scroll.in/article/941701/delhi-government-has-a-new-strategy-to-curb-monkey-attacks-an-area-wise-census>.
- Kennedy, U, A Sharma and C Phillips (2018): "The Sheltering of Unwanted Cattle, Experiences in India and Implications for Cattle Industries Elsewhere," *Animals: An Open Access Journal from MDPI*, Vol 8, No 5, p 64.
- Kumar, N, D Mohan, Y Jhala, Q Qureshi and F Sergio (2014): "Density, Laying Date, Breeding Success and Diet of Black Kites *Milvus Migrans* Govinda in the City of Delhi (India)," *Bird Study*, Vol 61, No 1, pp 1–8.
- Kumar, N, U Gupta, Y Jhala, A Gosler and F Sergio (2018a): "Habitat Selection by an Avian Top Predator in the Tropical Megacity of Delhi: Human Activities and Socio-religious Practices as Prey-facilitating Tools," *Urban Ecosystems*, Vol 21, No 2, pp 339–49.
- Kumar, N, Q Qureshi, Y Jhala, A Gosler and F Sergio (2018b): "Offspring Defense by an Urban Raptor Responds to Human Subsidies and Ritual Animal-feeding Practices," *PLOS ONE*, Vol 13, No 10, e0204549.
- Kumar, N, U Gupta, H Malhotra, Y Jhala, Q Qureshi, A Gosler and F Sergio (2019a): "The Population Density of an Urban Raptor Is Inextricably Tied to Human Cultural Practices," *Proceedings of the Royal Society B: Biological Sciences*, Vol 286, No 1900, doi: 10.1098/rspb.2018.2932.
- Kumar, N, Y Jhala, Q Qureshi, A Gosler and F Sergio (2019b): "Human-attacks by an Urban Raptor Are Tied to Human Subsidies and Religious Practices," *Scientific Reports*, Vol 9, No 1, p 2545.
- Kumar, V (2014): "Dog Catching Training Programme Conducted by SDMC, Delhi—Circular Letter for HAWOs/Co-opted Members of Delhi," Ministry of Environment, Forests and Climate

- Change, Government of India, New Delhi, http://awbi.in/awbi-pdf/dog_catching_trg.pdf.
- Lai, P, A Rawat, A Sagar and K Tiwari (2005): "Prevalence of Dog-bites in Delhi: Knowledge and Practices of Residents Regarding Prevention and Control of Rabies," *Health and Population Perspectives and Issues*, Vol 28, No 2, pp 50–57.
- Lloyd-Smith, J, D George, K Pepin, V Pitzer, J Pulliam, A Dobson and B Grenfell (2009): "Epidemic Dynamics at the Human-Animal Interface," *Science*, Vol 326, No 5958, pp 1362–67.
- Lloyd-Smith, J, P Cross, C Briggs, M Daugherty, W Getz, J Latto and A Swei (2005): "Should We Expect Population Thresholds for Wildlife Disease?" *Trends in Ecology & Evolution*, Vol 20, No 9, pp 511–19.
- MoF (2018): *Economic Survey 2018–19*, Ministry of Finance, Government of India, New Delhi, viewed on 22 July 2019, <https://www.indiabudget.gov.in/economicsurvey/>.
- MoI (2012): *19th Livestock Census-2012: All India Report*, Ministry of Industries, Government of India, New Delhi.
- Narayanan, Y (2019): "Jugaad and Informality as Drivers of India's Cow Slaughter Economy," *Environment and Planning A: Economy and Space*, Vol 51, No 7, pp 1516–35.
- Niemelä, J, J Breuste, G Guntenspergen, N McIntyre, T Elmqvist and P James (eds) (2011): *Urban Ecology: Patterns, Processes, and Applications*, Oxford: Oxford University Press.
- O'Connor, T P (2000): "Human Refuse as a Major Ecological Factor in Medieval Urban Vertebrate Communities," *Human Ecodynamics: Symposia of the Association for Environmental Archaeology*, G Bailey, R Charles and N Winder (eds), Oxford: Oxbow Books, pp 15–20.
- Petit-Boix, Anna, Pere Llorach-Massana, David Sanjuan-Delmás, Jorge Sierra-Pérez, Elisabet Vinyes, Xavier Gabarrell et al (2017): "Application of Life Cycle Thinking Towards Sustainable Cities: A Review," *Journal of Cleaner Production*, Vol 166, pp 939–51.
- Pica-Ciamarra, U (2005): "Livestock Policies for Poverty Alleviation: Theory and Practical Evidence from Africa, Asia and Latin America," *Pro-Poor Livestock Policy Initiative*, viewed on 22 July 2019, <https://assets.publishing.service.gov.uk/media/57a08c5e5274a27b2001129/PPLPIwp27.pdf>.
- Pinault, D (2008): "Raw Meat Skyward: Pariah-kite Rituals in Lahore," *Notes from the Fortune-telling Parrot: Islam and the Struggle for Religious Pluralism in Pakistan*, D Pinault (ed) London: Equinox, pp 108–21.
- Rose, H (1970): "The Development of an Urban Subsystem: The Case of the Negro Ghetto," *Annals of the Association of American Geographers*, Vol 60, No 1, pp 1–17.
- Saleemdeen, R, E zu Ermgassen, M Kim, A Balmford and A Al-Tabbaa (2017): "Environmental and Health Impacts of Using Food Waste as Animal Feed: A Comparative Analysis of Food Waste Management Options," *Journal of Cleaner Production*, Vol 140, pp 871–80.
- SCS Engineers and Abt Associates (2017): "Ghazi-pur Landfill Rehabilitation Report," prepared for East Delhi Municipal Corporation, on behalf of US Environmental Protection Agency and Climate and Clean Air Coalition Municipal Solid Waste Initiative, viewed on 25 July 2019, https://ccacoalition.org/sites/default/files/resources/2018_Ghazipur-Landfill-Rehabilitation-Report_SCS-Engineers.pdf.
- Simmons, J (1981): "Urban Systems: The New Regional Geography," *L'Espace Géographique*, Vol 10, No 2, pp 135–42.
- Singh, Paras (2017): "9 Dog Bite Cases Every Hour This Year," *Times of India*, 31 July, <https://timesofindia.indiatimes.com/city/delhi/9-dog-bite-cases-every-hour-this-year/articleshow/59837156.cms>.
- Sobsey, M D, L A Khatib, V R Hill, E Alcolija and S Pillai (2006): "Pathogens in Animal Wastes and the Impacts of Waste Management Practices on Their Survival, Transport and Fate," viewed on 22 July 2019, https://fyi.extension.wisc.edu/manureirrigation/files/2014/03/AS-ABE_2006_Pathogens-in-Animal-Wastes-and-Impacts-of-Waste-Management-Practices.pdf.
- Sorathiya, L, A Fulsoumar, K Tyagi, M Patel and R Singh (2014): "Eco-friendly and Modern Methods of Livestock Waste Recycling for Enhancing Farm Profitability," *International Journal of Recycling of Organic Waste in Agriculture*, Vol 3, No 1, p 50.
- Speedy, A (2003): "Global Production and Consumption of Animal Source Foods," *Journal of Nutrition*, Vol 133, No 11, pp 4048S–53S.
- Srivastava, S (2014): *Entangled Urbanism*, New Delhi: Oxford University Press.
- Talyan, V, R Dahiya and T Sreekrishnan (2008): "State of Municipal Solid Waste Management in Delhi, the Capital of India," *Waste Management*, Vol 28, No 7, pp 1276–87.
- Taneja, A (2015): "Sainly Animals: The Shifting Moral and Ecological Landscapes of North India," *Comparative Studies of South Asia, Africa and the Middle East*, Vol 35, No 2, pp 204–21.
- Tiwari, H, M O'Dea, I Robertson and A Vanak (2019): "Knowledge, Attitudes and Practices (KAP) Towards Rabies and Free-roaming Dogs (FRD) in Shirsuphal Village in Western India: A Community Based Cross-sectional Study," *PLOS Neglected Tropical Diseases*, Vol 13, No 1, e0007120.
- UN (2018): "World Urbanization Prospects: The 2017 Revision," United Nations, New York.
- WHO (2019): "Rabies and Neglected Tropical Diseases," viewed on 22 July 2019, <http://www.searo.who.int/india/topics/rabies/en/>.

EPWRF India Time Series Module on Health Statistics



Features

Presents All-India and state-wise annual data from 1980 onwards.

Structured in six major sections :

- Demography
- Health Status
- Infrastructure
- Human Resources
- Health Education
- Health Finance

The EPWRF ITS has 20 modules covering a range of macro-economic, financial and social sector indicators on the Indian economy

For more details, visit : www.epwrfits.in



Research team explaining scientific objectives and informing citizens of Delhi on the ecological importance of predatory kites (as well as other birds) while ringing kite chicks. This sort of citizen-group assembles constantly in a megacity of more than 16 million inhabitants like Delhi, as we move from nest to nest during our routine fieldwork activities, offering a unique opportunity to reach thousands of people in disseminating science, and educating the population on urban environmental issues of conservation importance. Since 2013, we have reached more than 50,000 citizens through this mobile conservation education initiative, which we see as a mobile laboratory. For many of these people, this may be one of their few opportunities to empathize and get in contact with nature, but our conversations with people have often surprised us by the depth of concern that they already have, for example for the decline in numbers of small birds that they have noticed over recent years.

3. Appendix

*[Typescript Journal Articles (2) and two
Comic Booklets in English and Hindi]*

No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring

Fabrizio Sergio^{1*}, Giacomo Tavecchia², Alessandro Tanferna¹, Lidia López Jiménez¹, Julio Blas¹, Renaud De Stephanis¹, Tracy A. Marchant³, Nishant Kumar^{4,5} and Fernando Hiraldo¹

¹Department of Conservation Biology, Estación Biológica de Doñana – CSIC, C/Americo Vespucio, 41092 Seville, Spain; ²Population Ecology Group, Institute for Mediterranean Studies (IMEDEA), CSIC-UIB, 07190 Esporles, Spain;

³Department of Biology, University of Saskatchewan, SK S7N 5E2 Saskatoon, SA, Canada; ⁴Edward Grey Institute of Field Ornithology, Department of Zoology, Oxford University, OX1 3PS Oxford, UK; and ⁵Wildlife Institute of India, Post Box # 18, Chandrabani, Uttarakhand 248001, India

Summary

1. The deployment of electronic devices on animals is rapidly expanding and producing leap-frog advances in ecological knowledge. Even though their effects on the ecology and behaviour of the marked subjects are potentially important, <10% of the studies are accompanied by an evaluation of impact, and comprehensive, long-term assessments have been few. Therefore, there is an urgent need to test for impacts, especially for tags that are heavy and deployed for long time periods, such as satellite transmitters.

2. We marked 110 individuals of a medium-sized, migratory raptor, the black kite *Milvus migrans*, with GPS satellite tags, representing about 4% of the body mass and attached as backpacks through a Teflon harness. Tagged individuals were compared to control animals of similar sex, age and breeding status for a large number of behavioural, condition-related and ecological traits.

3. Despite a sample size two- to threefold greater than most previous assessments that reported significant impacts, there was no detectable difference between tagged and control individuals in key vital rates such as survival probability, longevity, recruitment, age of first breeding, reproductive performance and timing of breeding.

4. Tagged and untagged kites showed similar social dominance during fights over food and a similar capability to provision nestlings, which prevented carry-over effects on the stress levels and condition of their offspring.

5. *Synthesis and applications.* Radio-marking studies are growing exponentially in the current ‘movement ecology era’, and impact assessments will be ever more important. In principle, tags of up to 4% mass-load can be deployed without apparent harm on some avian soaring species, but impacts should be properly evaluated on a case-by-case basis. Resilient species for which impacts seem weak could be used as early warning systems for trials of new devices: if impacts are observed, they are likely to be even greater on more vulnerable species. Finally, individual fatalities caused by marking should be taken into serious account, but comprehensively evaluated in the light of broader population-level impacts. Future initiatives to minimize tagging impacts could include more stringent licensing criteria enforcing attendance at training courses or incorporation of impact evaluations into study designs, increased availability of training courses for tagging, and enhanced sharing of information through blogs, workshops or specialized journal sections.

*Correspondence author. E-mail: fsergio@ebd.csic.es

Key-words: backpack attachment, GPS, harness, impact, *Milvus migrans*, movement ecology, radiomarking, satellite tagging, telemetry, vital rates

Introduction

The deployment of electronic data loggers such as radio-transmitters or geolocators is increasing greatly in animal ecology as a result of the rapid improvement in device size and cost, as well as the quality of the information obtained (Cooke *et al.* 2004; Wikelski *et al.* 2007; Rutz & Hays 2009). These new technologies are producing leap-frog advances in ecological knowledge and research opportunities. For example, satellite and GSM transmitters currently facilitate an unprecedented capability to monitor animal movement, behaviour and survival for several years over enormous areas (e.g. McGrady *et al.* 2003; Klaassen *et al.* 2013; Dodge *et al.* 2014). In turn, this facilitates estimates of migratory performance, survival rates and causes of mortality only dreamt of until very recently, as the biases generated by poor sampling of unpopulated, remote or inaccessible areas are virtually removed (e.g. Croxall *et al.* 2005; Burnham & Newton 2011; Klaassen *et al.* 2013). However, several recent studies have shown that marking animals with devices may alter their behaviour, energetics and vital rates (reviews in Calvo & Furness 1992; Murray & Fuller 2000; Godfray & Bryant 2003; Barron, Brawn & Weatherhead 2010). Commonly reported effects include higher energy expenditures and impaired foraging, survival and breeding success, with impacts varying among species or methods of device attachment, and becoming more evident under harsher environmental conditions (e.g. Marzluff *et al.* 1997; Barron, Brawn & Weatherhead 2010).

These known effects of marking emphasize the need to ensure that new devices do not affect the welfare of the study subjects or prejudice the quality of the data that they are designed to obtain by influencing behaviour (e.g. Casper 2009; Kenward 2001). However, <10% of studies based on marking devices incorporate an assessment of their potential impact on the subjects and this frequency has not increased through time (Murray & Fuller 2000; Godfray & Bryant 2003). This is particularly worrying for four reasons.

1. Rapid technological developments cause researchers to 'jump' on new-generation, cutting-edge devices and this is often not accompanied by proper testing of impacts because of the pressure to produce novel results quickly.

2. Heavier devices, such as satellite or GSM tags, produce very attractive information at high costs, which leads to small samples of tracked animals that are frequently hard to capture. This leads to studies in which researchers want to maximize battery life (and thus device load) to optimize costs and field effort, but are unable to test for deleterious effects because of small samples (usually <7–10 individuals).

3. Indications of maximum admissible mass-loads are often vague, arbitrary, or based on few assessments, which makes many researchers lax about them. For example, in birds maximum suggested loads vary from 1% to 5%, with no clear agreement (e.g. Murray & Fuller 2000; Kenward 2001; Barron, Brawn & Weatherhead 2010).

4. Finally, most evaluations have examined a small set of short-term life-history parameters, which makes it unclear whether the demonstrations of low impact could be caused by the short duration of the assessment or by compensatory behaviours by the subjects (e.g. higher breeding performance at the expense of longer-term survival, or impact compensated for by higher foraging effort by an untagged partner; Barron, Brawn & Weatherhead 2010).

For all the above reasons, there is an urgent need to accompany radio-marking studies with comprehensive evaluations of their tagging impacts, in order to ensure a critical mass of results essential to produce robust meta-analyses and generalizations, as strongly requested in all recent reviews of the subject, which lament the lack of information (Calvo & Furness 1992; Murray & Fuller 2000; Barron, Brawn & Weatherhead 2010). Here, we take advantage of a long-term demographic study on a long-lived raptor, the black kite *Milvus migrans*, to test the impact of a large-scale satellite-marking programme (Sergio *et al.* 2014) on an unusually comprehensive suite of behavioural and life-history traits. The black kite is a medium-sized, opportunistic, migratory raptor. Kites are sexually monomorphic in size, but females are 15% heavier on average than males (Sergio *et al.* 2007a). The age of first breeding varies between 1 and 7 years, and the maximum known longevity is 28 years (Sergio *et al.* 2011a). We consider our study of general interest for the evaluation of tagging impacts for five reasons.

1. Transmitters were attached as backpacks using harnesses, which allow a longer period of radiodeployment, but can cause injuries (Kenward 2001), and their use is likely to spread as tags become longer-lasting.

2. Harness attachments have been shown occasionally to cause severe injuries in a threatened, congeneric and morphologically similar species, the red kite *Milvus milvus*, but no assessment of an overall population impact could be conducted (Peniche *et al.* 2011).

3. The black kite is one of the commonest soaring migrants (Newton 2008), so that information on potential data biases produced by satellite tagging could be relevant for other tracking studies on migration.

4. Satellite tags, such as those used here, are on average heavier and larger than other transmitters, but their impact has seldom been evaluated (e.g. Phillips, Xavier & Croxall 2003; Therrien, Gauthier & Bêty 2012), usually

because their high costs mean that too few animals are marked for meaningful comparisons to be made.

5. The incorporation of a large-scale tagging programme into a long-term intensive demographic study provides an ideal setting for a detailed evaluation of impact on a comprehensive suite of vital parameters, preventing the possibility that compensatory behaviours obscure real impacts.

Materials and methods

FIELD PROCEDURES: TRAPPING, SATELLITE TAGGING AND POPULATION MONITORING

We trapped 92 adult kites for radiomarking by cannon-netting them on baited carrion between March and June 2007–2013 in Doñana National Park (south-western Spain). In addition, we tagged 18 nestlings (each from a different nest) in their last week before fledging (40- to 48-day-old nestlings; Viñuela & Bustamante 1992). Kites were marked with GPS satellite tags (model PTT-100 Solar Argos/GPS PTT of 22 g, manufactured by Microwave Telemetry, Inc., Columbia, MD, USA), by attaching them as backpacks through a 6-mm-wide tubular Teflon harness (Kenward 2001). The cumulative mass of the tag and complete harness was 29.8 g, that is 3.77% of the mass of the marked kites.

More than 4000 black kites have been banded as nestlings in Doñana National Park since the 1970s, so that a large proportion of the population is composed of intensively monitored, known-age individuals, whose plastic rings can be read from far with a telescope (e.g. Blas, Sergio & Hiraldo 2009; Sergio, Blas & Hiraldo 2009a; Sergio *et al.* 2011a). Each year, we collected large numbers of ring readings for the whole population throughout the breeding season by regularly observing kites at their territories, at communal roosts and at trapping sites baited with carrion (Blas, Sergio & Hiraldo 2009; Sergio, Blas & Hiraldo 2009a; Sergio *et al.* 2009b, 2011a). This constantly high ring-reading effort allowed us to follow the fate of all ringed and satellite-tagged individuals even after the satellite tags stopped working. The nests of all breeding individuals were checked approximately every 2 weeks to estimate their breeding performance. Whenever possible, we ringed the nestlings of all pairs with a marked parent when they were approximately 35–40 days old and measured their body mass to the nearest 5 g, tarsus length to the nearest 0.1 mm, and wing length to the nearest 1.0 mm. Nestling age at ringing was estimated through a linear regression equation of chick age on the length of the eighth primary feather (Viñuela & Bustamante 1992). For each nestling, we collected two supracaudal feathers from the rump to estimate stress levels through subsequent corticosterone analysis, following the same procedures detailed by Bortolotti *et al.* (2008) and López-Jiménez *et al.* (2015). All birds trapped as adults or ringed as nestlings were sexed by molecular analysis of a blood sample.

To examine the impact of tagging on the capability to monopolize food in a competitive social environment (social dominance), we conducted standardized observations of individuals feeding and fighting on baited carrion (hereafter 'feeding observations'; Sergio *et al.* 2011b). In each observation session, we placed 30–35 skinned sheep heads of equal dimensions in a 10×10 m quadrat. Once a marked individual was feeding on a bait item, an observer placed in a hide c. 10 m away recorded for 10 min: (i) the number of times it was attacked by other individuals

trying to displace it from the food and their success; (ii) if displaced, the number of times it attacked other individuals to displace them and their success; and (iii) the cumulative proportion of time spent eating (i.e. the time it managed to monopolize food in a competitive environment) (Sergio *et al.* 2011b).

To estimate the effect of tagging on ability to provision offspring, we placed camera traps at 20 nests ($N = 68$ complete days of data): 10 nests with a satellite-tagged male and 10 nearby control nests with an untagged male. We focused exclusively on males, because in our population they are the main and almost sole providers of food for the nestlings (Sergio *et al.* 2007a). All camera traps had an infrared sensor that triggered the camera whenever it detected movement in the nest. This allowed us to record all the prey items delivered and fed to the nestlings by the parents.

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSES

To estimate the impact of tagging, each satellite-marked kite (hereafter 'satellite individual') was compared to a control individual that (i) was ringed but untagged, (ii) was of the same sex as the satellite kite, (iii) had the same age and breeding status (breeder or floater) in the year of trapping of the satellite kite (i.e. the history of the two birds was aligned to start from the same year and the same age and status conditions), and (iv) bred within the same general area of the park, if it was a breeder (i.e. within the same sector, as defined in Sergio *et al.* 2011c). In the few cases in which the age condition could not be satisfied, we looked for the next closest individual available and alternated equally between younger and older control birds in order to minimize age biases. Thus, for example, if control individuals of the exact same age were not available for two satellite kites of age x and y , for the first we chose a control individual of age $x + 1$ and for the second an individual of age $y - 1$. Because control birds had not been trapped, we defined the year of trapping of their satellite counterpart as the year of their (virtual) trapping.

Survival of satellite and control individuals was estimated using capture–recapture models (Burnham *et al.* 1987). Analyses were run separately for breeding and floating individuals to test whether tagging affected the two groups in different ways. Within each group, we followed the same age-structure retained by an information-theoretic approach in the detailed capture–recapture models reported in Sergio *et al.* (2011a), with ageclasses of 1, 2 and 3–6 years old for floaters and of 3–6, 7–11 and 12–28 years old for breeders. The statistical relevance of carrying a satellite tag was assessed using a likelihood ratio test (LRT) between a model assuming an effect of the tag and a model assuming the same survival probability for tagged and untagged kites (Burnham *et al.* 1987). A LRT was preferred to the model information approach based on Akaike Information Criterion (AIC) because we were interested only in testing the effect of the tag. For an extensive description of modelling kite survival, we refer to Sergio *et al.* (2011a).

For all other analyses, we used generalized linear mixed models (GLMMs; Zuur *et al.* 2009) to test the impact of tagging on vital rates and behaviour. Year, individual identity, or nest identity were fitted as random factors to control for pseudoreplication or for their potentially confounding effect (Table 1). In all models, we were interested in testing the following predictions: (i) behavioural and demographic performance are lower in tagged than in control individuals; (ii) such impacts are stronger in certain

Table 1. Hypotheses and predictions of the impact of satellite tagging on several life-history, ecological and behavioural traits of individual black kites

Trait tested for impact ^a	Explanatory variables ^b	Hypothesis Tagging affects:	Prediction Significant effect of:
a. Adult mass	Tagging, sex, age, date, time-lag from 1st trapping ^c	The body mass of the radio-marked adult Adult body mass depending on sex Adult body mass depending on age Adult body mass, but its effect increases with time	Tagging Tagging × sex Tagging × age Tagging × time-lag
b, c. Survival ^d	Tagging, sex, age	Survival Survival depending on sex Survival depending on age	Tagging Tagging × sex Tagging × age
d. Longevity	Tagging, sex, status, age at trapping ^{e,f}	Longevity Longevity depending on sex Longevity depending on status Longevity depending on age at tagging	Tagging Tagging × sex Tagging × status Tagging × age
e. Recruitment ^g	Tagging, sex, age ^c	Annual recruitment ^g The recruitment of floaters depending on sex The recruitment of floaters depending on age	Tagging Tagging × sex Tagging × age
f. Recruitment ^h	Tagging, sex, age at trapping ^f	Cumulative recruitment ^h The recruitment of floaters depending on sex The recruitment of floaters depending on age at tagging	Tagging Tagging × sex Tagging × age
g. Age at 1st breeding	Tagging, sex, age at trapping ^f	Age at first breeding (age 1st breed) The age 1st breed of floaters depending on sex The age 1st breed of floaters depending on age at tagging	Tagging Tagging × sex Tagging × age
h,i,j. Productivity ⁱ	Tagging, period ^j , sex, age ^c	Productivity ^j Productivity ^j depending on sex Productivity ^j depending on age	Tagging × period Tagging × period × sex Tagging × period × age
k,l. Social competence ^k	Tagging, sex, age, date	Social competence ^k Social competence ^k depending on sex Social competence ^k depending on age	Tagging Tagging × sex Tagging × age
m. Provisioning rates	Tagging, age ^l , date, brood size, nestling age	Nestlings provisioning rates Provisioning rates depending on parental age The provisioning rates at broods of 1 vs. 2 nestlings	Tagging Tagging × age Tagging × brood size
n. Nestlings' body mass	Tagging, age, brood order, nestling age, tarsus length	Nestlings' body mass at ringing Nestlings' mass depending on sex of the marked parent Nestlings' mass depending on age of the marked parent	Tagging Tagging × sex Tagging × age
o. Nestlings' Cort ^m	Tagging, age, brood order, chick age, chick condition ⁿ	Nestlings' feather-corticosterone levels (Cort) Nestlings' Cort depending on sex of the marked parent Nestlings' Cort depending on age of the marked parent	Tagging Tagging × sex Tagging × age

^aDependent variable in each model. The letters that identify each model (a, b, c, etc.) correspond to those in Table 2.

^bExplanatory variables fitted to the model to control for confounding factors that could obfuscate the effect of tagging (the interactions fitted to each model are specified in the column 'Prediction').

^cIndividual identity and year were fitted as random factors.

^dSurvival of both floaters and breeding kites: the hypotheses and predictions were the same for both models.

^eBreeding status (1 = floater, 2 = breeder).

^fIndividual identity was fitted as a random factor.

^gAnnual recruitment: probability that a floater will recruit in a given year.

^hCumulative recruitment: whether a floater recruited or died within 7 years of age.

ⁱIncludes models with laying date, clutch size or number of fledged young as dependent variables.

^jBreeding attempts before or after the tagging episode. The inclusion of this variable allowed to test whether differences in productivity between satellite and control individuals before tagging were amplified or reduced after radiomarking.

^kIncludes models with the capability of fighting or of monopolizing food in a competitive social group as dependent variables.

^lAge of the parent bird. Sex was not fitted because the analysis focused exclusively on males (the main food-providing sex).

^mCorticosterone levels in feathers (pg mm⁻¹).

ⁿResiduals of a regression of the nestlings' body mass on their age and tarsus length.

ageclasses (e.g. in younger inexperienced individuals, or in older birds because of the added cost of breeding); and (iii) tagging impacts are stronger in males because they receive larger loads due to their lower mass and have higher metabolic costs during breeding as they are the main food providers for the whole family. Therefore, we fitted to all models the variable 'tagging' (whether an individual was a satellite or control kite) and its interaction with age and sex. Other covariates included in the

models are detailed in Table 1 and were chosen based on accumulated knowledge about the study population in order to control for confounding factors potentially affecting each dependent variable and thus obfuscating tagging effects.

To analyse the impact of tagging on longevity, we proceeded as follows: capture–recapture models provided an estimate of recapture probability for untagged birds, defined as the probability to resight a bird at a specific time *i*, given that it has survived

Table 2. GLMM and capture–recapture models testing the impact of satellite tagging on the body condition, vital rates, social dominance and the capability of adequately provisioning the offspring by black kites. All analyses are based on the comparison of satellite-tagged kites and control individuals of the same sex, age and site quality (see Materials and methods)

Variable	<i>n</i>	ΔAkaike Information Criterion (AIC) ^a	LR test ^b	<i>P</i>
a. Dependent variable: adult body mass ^{c,d}	46			
Tagging ^e		−1.78	0.23	0.63
Tagging × sex		−1.86	0.14	0.72
Tagging × age		−1.91	0.08	0.78
Tagging × time-lag ^f		−1.73	0.27	0.60
b. Dependent variable: survival floaters ^g	80 ^h			
Tagging ⁱ		−1.01	1.15	0.28
Tagging × sex		−1.63	0.65	0.42
Tagging × ageclass		−3.92	0.62	0.73
c. Dependent variable: survival breeders ^g	114 ^h			
Tagging ⁱ		−0.26	1.99	0.16
Tagging × sex		−8.22	1.64	0.95
Tagging × ageclass		−0.26	1.99	0.16
d. Dependent variable: longevity ^j	48			
Tagging ⁱ		−1.98	0.01	0.92
Tagging × sex		−2.00	<0.01	0.99
Tagging × status ^k		−1.85	0.15	0.70
Tagging × age ^l		−1.89	0.11	0.74
e. Dependent variable: annual recruitment ^m	80 ⁿ			
Tagging ⁱ		−1.99	0.01	0.92
Tagging × sex		−1.95	0.05	0.82
Tagging × ageclass		−1.58	1.42	0.23
f. Dependent variable: cumulative recruitment ^m	42 ^o			
Tagging ⁱ		−1.92	0.08	0.78
Tagging × sex		−1.91	0.09	0.77
Tagging × ageclass		−1.84	0.16	0.69
g. Dependent variable: age of first breeding ^d	46			
Tagging ⁱ		−1.99	0.01	0.94
Tagging × sex		−1.99	0.01	0.92
Tagging × age ^l		−1.95	0.04	0.84
h. Dependent variable: Laying date ^d	126			
Tagging ⁱ		−1.82	0.18	0.67
Tagging × period		−3.96	0.04	0.98
Tagging × period × sex		−1.88	0.13	0.72
Tagging × period × age		−0.14	1.86	0.17
i. Dependent variable: Clutch size ^j	128			
Tagging ⁱ		−1.97	0.03	0.86
Tagging × period		−1.63	0.37	0.55
Tagging × period × sex		−5.22	0.78	0.85
Tagging × period × age		−10.43	1.57	0.95
j. Dependent variable: number of fledged young ^j	200			
Tagging ⁱ		−1.65	0.34	0.56
Tagging × period		−1.98	0.02	0.89
Tagging × period × sex		−4.90	1.10	0.78
Tagging × period × age		−5.47	0.53	0.91
k. Dependent variable: social dominance ^{d,p}	48			
Tagging ⁱ		−2.01	0.01	0.99
Tagging × sex		−1.21	0.79	0.37
Tagging × ageclass		−2.82	1.18	0.55
l. Dependent variable: fighting capability ^{d,q}	48			
Tagging ⁱ		−1.69	0.31	0.58
Tagging × sex		−1.99	0.01	0.93
Tagging × ageclass		−3.24	0.77	0.68
m. Dependent variable: nestling provisioning rates ^{d,r}	68			
Tagging ⁱ		−1.95	0.04	0.84
Tagging × brood size		−1.83	0.16	0.68
Tagging × ageclass		−1.16	0.84	0.36

(continued)

Table 2. (continued)

Variable	<i>n</i>	ΔAkaike Information Criterion (AIC) ^a	LR test ^b	<i>P</i>
n. Dependent variable: nestlings' body mass at ringing ^d	78			
Tagging ⁱ		−1.95	0.05	0.82
Tagging × sex ^s		−4.22	1.78	0.62
Tagging × ageclass		−5.29	2.71	0.61
o. Dependent variable: nestlings' corticosterone levels ^d	58			
Tagging ⁱ		−1.93	0.08	0.78
Tagging × sex ^s		−1.78	0.22	0.64
Tagging × ageclass		−2.14	1.86	0.39

^aChange in AIC value when removing the variable from the maximal model (see Materials and methods). Negative values indicate that the model fit improved upon removal of the variable from the model. In all cases, the same results were obtained when adding the variable to the minimal model or to the null model.

^bLikelihood ratio test of the change in deviance upon removal of the variable from the maximal model.

^cBody mass of individuals that were recaptured later in life after radiotagging.

^dLinear mixed model with Gaussian errors and an identity link function.

^eTagging treatment: for this model, 1 = measurement at first capture (i.e. just before radiotagging); 2 = measurement (without radiotag) upon its recapture later in life.

^fTime-lag between the first and second capture of the same individual.

^gSurvival models were implemented in MARK for individuals captured as breeders or as floaters (i.e. non-breeding individuals).

^hFloaters: *N* = 40 satellite-tagged vs. 40 control individuals; breeders: *N* = 57 satellite-tagged vs. 57 control individuals.

ⁱTagging treatment: 1 = satellite-tagged bird; 2 = control individual.

^jGeneralized linear mixed model with Poisson errors and a logarithmic link function.

^kBreeding status at capture: 1 = floater; 2 = breeder.

^lAge at the time of tagging.

^mGeneralized linear mixed model with binomial errors and a logit link function.

ⁿAnalysis based on *N* = 192 recruitment episodes (each year in which a previously floater individual was known to be alive and either recruited or not) from 40 satellite-tagged vs. 40 control individuals.

^oAnalysis based on *N* = 21 satellite-tagged vs. 21 control individuals which recruited or not within their initial 7 years of life.

^pCapability to monopolize food in a competitive social group, as estimated by the proportion of time spent eating in a group of conspecifics during 10-min bouts of observation (arcsine square-root transformed).

^qProportion of times that an individual succeeded in either dislodging another individual from a food item or to defend it from an attacker (arcsine square-root transformed).

^rBiomass of prey delivered to the nestlings per day (*N* = 68 full days of camera-trapping from 10 nests of satellite-tagged males and 10 nests of control individuals).

^sSex of the parent individual.

the previous time interval, from *i*−1 to *i*. In particular, the detection probability of untagged birds was 0.97 per year for breeding kites and 0.72 for non-breeding kites. Thus, the probability that an unmarked breeding bird estimated to be alive was in the population for two consecutive years without being seen was very low at $(1-0.97)^2 = 0.0009$. This figure was 0.08 for a non-breeding kite and dropped to 0.02 for a bird not seen for three consecutive years. Based on the above, we classified an individual as dead if it was (i) physically recovered as such, (ii) a breeder not seen for two consecutive years or (iii) a non-breeder not seen for three consecutive years. For individuals classified as dead according to the above criteria, we then examined the effect of carrying or not a satellite tag on observed longevity, defined as the age of an individual when it was classified as dead (i.e. its age when last observed; Table 1). All individuals of uncertain status (e.g. not seen for only 1 year) were discarded from analysis.

Similarly, because the detectability of breeders was extremely high, we classified a bird as recruited if it was observed holding a territory and as a floating bird if it was known to be alive that year (e.g. because it was regularly observed at roosts, or seen alive in subsequent years) but was never observed holding a territory. Non-recruited individuals not observed for 3 years or more at the end of the study or not observed in the final 2 years of the study were discarded from recruitment analyses because

they were estimated as dead (see above), or to avoid biasing results by including false zeros (i.e. individuals that could appear as still alive in subsequent years). We then explored the effect of tagging on the probability that a floating individual would recruit or not in each individual year in which it was known to be alive (defined as 'annual recruitment'; Table 1). To provide a longer-term and more comprehensive measure of recruitment efficacy, we also tested whether tagging affected the probability that an individual would recruit within its first 7 years of life (7 years is the maximum age of first breeding in our population; Sergio, Blas & Hiraldo 2009a). We define this as 'cumulative recruitment' and included in this analysis: (i) individuals known to have recruited; and (ii) individuals that were unknown to have recruited but would have reached 7 years of age within the end of the study. Therefore, each individual appeared only once in this analysis.

For estimates of reproductive timing and success, data were also available for the longitudinal performance of each satellite and control individual before and after the tagging year (not available for other traits because, for example, survival is 1 by default before trapping). This allowed us to implement a full before–after control–impact (BACI) test by checking whether the performance was similar between the two groups both before and after tagging. Thus, in these analyses, an impact of satellite

marking was revealed by a significant interaction between 'tagging' (whether an individual was a satellite or control kite) and 'period' (i.e. before vs. after 'the tagging year', Table 1; see Gregory, Gordon & Moss 2003 for a similar design).

For feeding observations, it was often impossible to find adequate control individuals of the same age within the few hours of each observation day. So, whenever a satellite-tagged individual was present, we recorded its performance and compared it to the one of the ringed, untagged individual observed just before or after the tagged focal individual. Age was then controlled simply by fitting it as a covariate. Similarly, for nest provisioning rates, we opportunistically chose as control nest a nearby one occupied by a ringed untagged male.

In Table 1, we give details of the explanatory variables fitted to the models, and of the hypotheses and predictions testing the impact of tagging. All models were built through a backward stepwise procedure following Zuur *et al.* (2009): all explanatory variables were fitted to a maximal model, extracted one at a time from such maximal model, and the associated change in model deviance was assessed by a LRT; at each step, we also calculated the AIC of each model and considered as the final competitive model the one with the lowest AIC containing only significant terms. Variables with a $\Delta AIC < 2$ upon removal or with $P > 0.05$ in the LRT were considered as non-significant.

In all analyses, age was fitted as a linear, quadratic or categorical variable (with levels: 1–2, 3–6, 7–11 and 12–27 years old), based on which gave the best fit to the maximal model, as detailed in Sergio *et al.* (2014). Details of the error distribution of each model are given in the footnotes of Table 2. In all models, we assessed collinearity by examining the variance inflation factor (VIF) values of the explanatory variables, which were always low (< 1.3 ; Crawley 2007; Zuur *et al.* 2009). To avoid over-parameterization, we ensured never to fit more than $N/3$ variables to each maximal model (Crawley 2007). Overdispersion was never detected and model assumptions were checked by looking at QQ plots, histograms of residuals, and plots of standardized and normalized residuals against fitted values and against explanatory variables, or by incorporating variance structures VarIdent or VarFixed (Crawley 2007; Zuur *et al.* 2009). All GLMMs were implemented in R 3.0.2 (R Development Core Team 2009) and all capture-recapture models in MARK (White & Burnham 1999). All tests are two-tailed, statistical significance was set at $\alpha < 0.05$, and all means are given ± 1 SE.

Results

A single individual removed its harness 4 months after marking (0.9% of 110 tagged individuals). Of 42 individuals re-trapped or recovered freshly dead up to 4 years after tagging, one had an abrasion below the ventral T-junction of the harness, caused by an unusually tight-fitting ventral loop of the harness, similar to that described by Sunde (2006), but less severe than the injuries reported by Peniche *et al.* (2011). The re-trapped bird was freed from the incorrectly placed harness and went on to successfully raise young. In all the recovered birds, the skin under the transmitter was always featherless but intact, with no sign of inflammation or previous injury. No other signs of injury were evident and the body mass of the tagged birds was similar at marking and when

re-trapped, independently of the time-lag between the two (Table 2a; Fig. 1).

For both breeding and non-breeding kites, there was no difference in the survival of tagged and control individuals, and no significant interaction between marking treatment and age or sex (Table 2b,c; Fig. 2). The duration of the study prevented a similar analysis for birds tagged as nestlings, but the remotely recorded survival of the satellite birds to 1 year of age was 0.421 ± 0.116 ($N = 18$), that is similar to the 0.407 estimate based on ring recoveries for the same population (Sergio *et al.* 2011a). For birds that died during the course of the study, there was no difference in mean longevity between tagged and control individuals, independently of their age or sex (Table 2d; Fig. 3).

The annual and cumulative recruitment of floating kites into the breeding population and their age of first breeding were not affected by tagging, nor by its interaction with age or sex (Table 2e,f,g; Figs 2 and 3). Similarly, laying date, clutch size and the number of young raised to fledging did not vary with tagging or its interaction with age or sex (Table 2h,i,j; Fig. 4).

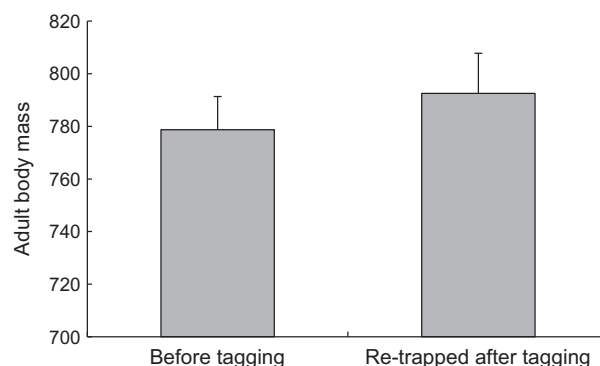


Fig. 1. Body mass of 23 adult black kites when trapped for satellite tagging and of the same 23 individuals upon re-trapping after radiotagging. Bars represent means ± 1 SE.

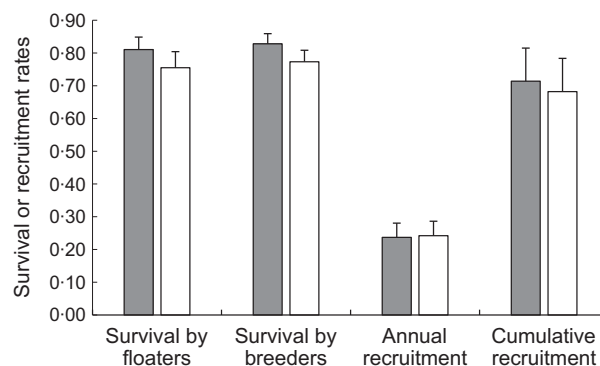


Fig. 2. Survival and recruitment rates of satellite-tagged black kites (grey bars) and control individuals (white bars). Annual recruitment is the probability that a floater will recruit in a given year, while cumulative recruitment is the probability that it will recruit within its seventh year of life. Bars represent mean ± 1 SE.

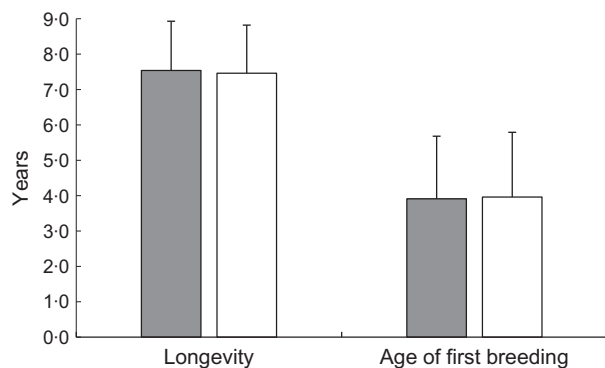


Fig. 3. Age of first breeding and longevity of satellite-tagged black kites (grey bars) and control individuals (white bars). Bars represent mean + 1 SE.

The proportion of time spent eating carrion, the capability to evict other kites from a food item or to defend it, and nestling provisioning rates did not differ between satellite and control birds (Table 2k,l,m; Figs 5 and 6). Finally, the body mass at ringing and the corticosterone levels of the nestlings did not vary with the tagging of their parents or its interaction with parental age or sex (Table 2n,o; Fig. 6).

Discussion

We found no evidence of a marked impact of satellite tagging on black kites. Social dominance over food and foraging performance, as assessed by provisioning rates, were unaffected by tagging, suggesting that the added load and drag did not excessively impair flight capabilities. As a result, the body mass of marked birds was maintained, even after several years of wearing a tag. Similarly, key vital rates, such as survival, recruitment, age of first breeding and reproductive success, were not related to marking, which ultimately resulted in similar longevity between satellite and control individuals. Finally, tagging did not delay reproduction or reduce the condition of raised offspring. All the above relationships were independent of the age, sex, or status of the marked animal, suggesting that there were no socio-ecological characteristics which made an individual more prone to suffer a cost of tagging. In summary, there was no evidence of an impact on foraging and social behaviour, on the capability to proceed through key life stages and survive to breed, and no apparent carry-over effect on the viability of the offspring produced.

We doubt that the above results could be artefacts for five reasons.

1. The magnitude of all differences between satellite and control kites was so small and the overlap in measures of variation so large, that only a very extreme data bias could have reversed the results. We cannot think of such a source of bias. In fact, if anything, satellite kites performed slightly better than control individuals in many key comparisons, as reported in a recent meta-analysis (Barron, Brawn & Weatherhead 2010).

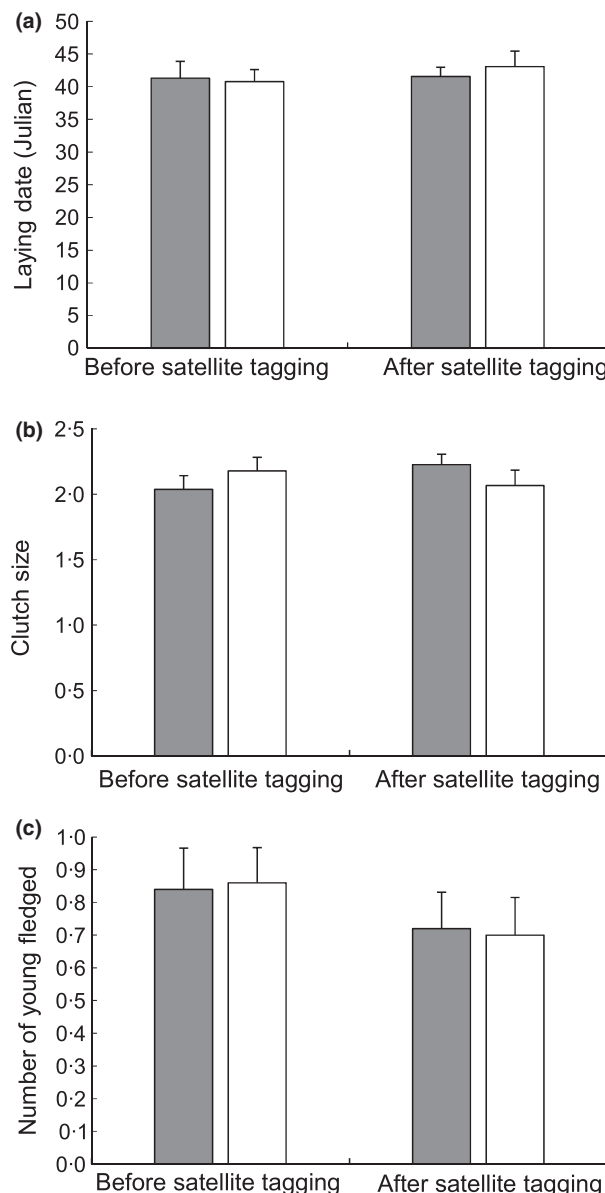


Fig. 4. Timing of breeding (a), clutch size (b) and number of young raised to fledging age (c) by satellite-tagged black kites (grey bars) and control individuals (white bars), before and after being trapped and radio-marked. Bars represent mean + 1 SE.

2. The sample size and duration of the study were two- or threefold larger than those of most previous studies that did detect significant impacts (reviews in Calvo & Furness 1992; Murray & Fuller 2000; Barron, Brawn & Weatherhead 2010).

3. Compared to previous evaluations, the study was unusually comprehensive in testing differential impacts by sex, age and breeding status on a larger than usual set of vital parameters and behaviours.

4. The systematic absence of impact in the whole comprehensive set of parameters analysed does not support the possibility that behavioural compensation obscured impacts by relegating them to unmeasured parameters. For example, there was no evidence that the absence of a

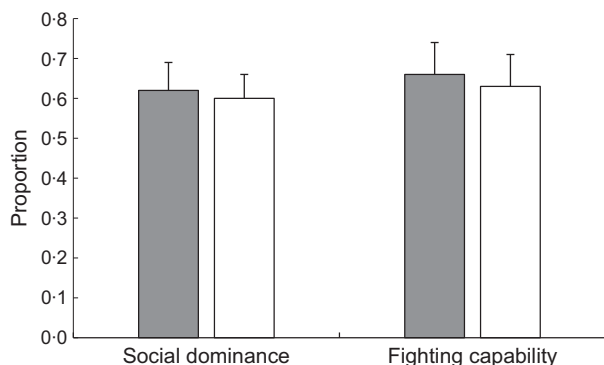


Fig. 5. Social competence of satellite-tagged black kites (grey bars) and control individuals (white bars). Social dominance was the ability to monopolize food in a competitive social group, and fighting capability was the percentage of successful defensive and offensive interactions with conspecifics over food. Bars represent mean $\pm$ 1 SE.

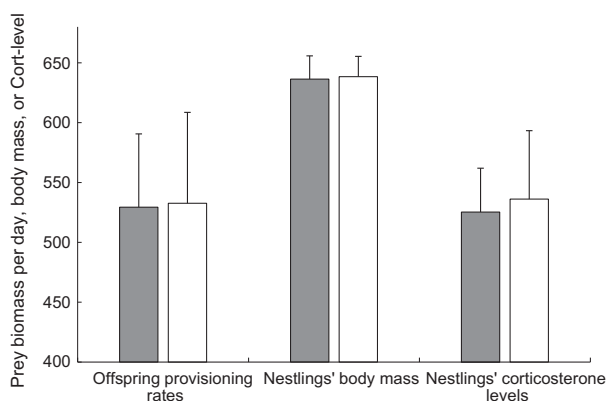


Fig. 6. Prey provisioning rates by adults to their nestlings (grams of prey delivered per day), and offspring body mass (in grams) and corticosterone (Cort) levels in feathers (pg mm^{-1}) for nests of satellite-tagged black kites (grey bars) and control individuals (white bars). Corticosterone levels were multiplied by 50 for clarity of presentation. Bars represent mean $\pm$ 1 SE.

tag effect on survival was attained through lower breeding effort or that sustained breeding success was maintained at the expense of offspring condition. A similar absence of compensatory mechanisms has been suggested by a recent meta-analysis (Barron, Brawn & Weatherhead 2010).

5. Finally, in the presence of a tagging impact, we would expect the performance of marked birds to deteriorate progressively through the years, as cumulative deleterious effects become more evident. On the contrary, most individuals improved their performance in successive years (as they aged and accumulated experience) in the same ways and with the same outcomes that had been previously described for ringed but non-radio-tagged kites of the same population. Thus, for example, individuals arrived progressively earlier at the breeding quarters in successive years and this translated into advantages for recruitment and reproduction (Sergio *et al.* 2007b; Sergio, Blas & Hiraldo 2009a; Sergio *et al.* 2014). Therefore, tagging did

not prevent us from capturing a realistic snapshot of the demographic functioning and life-history strategies of the population. All in all, if tagging effects were present in our population, they were likely to be of very limited magnitude and difficult to detect over the analysed time period.

Previous evaluations of the impact of backpack transmitters on birds of prey have reported significant effects on breeding performance (Foster *et al.* 1992; Marzluff *et al.* 1997; Gregory, Gordon & Moss 2003; Rodríguez *et al.* 2009) or on survival (Gervais *et al.* 2006; Steenhof *et al.* 2006), or both (Paton *et al.* 1991), or no detectable effect on breeding (Vekasy *et al.* 1996; Sunde 2006; Therrien, Gauthier & Bêty 2012) or survival (Foster *et al.* 1992; Reynolds *et al.* 2004; Sunde 2006; Rodríguez *et al.* 2009). Note that evaluations of satellite impacts have been almost non-existent (Steenhof *et al.* 2006; Therrien, Gauthier & Bêty 2012), despite much marking. Our results confirm that satellite marking may not be particularly deleterious in some cases. However, we express extreme caution in extrapolating the results of this study uncritically to other species for several reasons. First, the black kite has been defined as the paradigm of the generalist species (Viñuela 2000); it can kill prey ranging from a mosquito to a live 1-kg adult rabbit *Oryctolagus cuniculus* (authors' pers. obs.) and is considered to be the most numerous and successful raptor in the world (Ferguson-Lees & Christie 2001). As such, it may be better able to absorb the impact of tagging than others less generalist species. Secondly, it is a migratory, highly opportunistic predator adapted to exploit sudden flushes of food and to withstand periods of prey scarcity (Viñuela 2000). Its body mass thus fluctuates widely, with recorded mass variations of more than 250 g within individuals over the course of a few months (Sergio *et al.* 2009b; authors' unpublished data), that is more than eight times the tagging load. This may make this species well pre-adapted to withstand load additions. Thirdly, black kites are soaring migrants dependent on thermals (Newton 2008) and the breeding and wintering quarters of the study population are located in arid or semi-arid, generally warm areas, where thermal uplift may be common and strong, thus dampening the energetic costs of carrying an additional load. Other species or even other black kite populations that breed in colder climates and experience longer migrations could show larger impacts. Lastly, cumulative effects may only be visible over even longer time periods, through longer-term assessments that will only be available in future years as our study continues.

CONCLUSIONS AND APPLICATIONS

Although radiotagging may be sufficiently harmless in some contexts, even for transmitter loads up to almost 4% of body mass, evaluations of impact will be increasingly important as progressive improvements in device costs and miniaturization broaden the range and abundance of tagged species (e.g. Wikelski *et al.* 2007). In

the future, resilient species or populations like ours could be used as 'early warning systems' to test the viability of different transmitter types and loads because, if impacts are observed in these model species, they will be even more likely to occur in more exacting species. This could minimize unethical impacts and waste of funds and data in projects on threatened or more delicate taxa. Finally, the only adverse effect observed in this study was caused by one misplaced, excessively tight-fitting harness. This finding raises two issues. First, radiomarking through harnesses is likely to become more common because it is conducive to longer-term deployment and researchers will increasingly fit tags capable of functioning for years, yet harness-fitting is known to require experienced personnel (Kenward 2001) as poor practice can be harmful (e.g. Peniche *et al.* 2011). Secondly, mistakes are probably inevitable in any marking programme (Kenward 2001) and, however dramatic individual instances may be, decisions about the suitability of methods should be accompanied by broader assessments of comprehensive demographic impacts. Consequently, because occasional casualties or harm directly or indirectly caused by marking can have an impact with the public, it is important that scientists can provide explanations based on quantitative assessments, rather than qualitative reasoning.

Various initiatives could help to improve the issues raised above. First, tagging licences could be issued through more stringent criteria, such as demonstration of attendance at training courses, previous successful experience with the technique, or explicit incorporation of an impact evaluation into the project design. Secondly, high-quality training should be enhanced through more specialized courses (e.g. at congresses). Thirdly, sharing of information among users should be fostered through specialized blogs, forums or workshops, or by creating *ad hoc* sections in journals focusing on biotelemetry and animal movement. Fourthly, journal editors could demand that authors of telemetry studies should incorporate impact evaluations into their work as an essential component of study design. Finally, for studies constrained by funding limitations to fewer than 10 tagged individuals, for which impact evaluations will be difficult, we recommend that researchers use tags weighing <3%, and preferably 1%, of the body mass, that they use tagging methods previously tested on similar species, and that they explicitly express caution about the validity of their data as impact evaluations could not be implemented. Note that, with such small samples, adverse impacts even on a single individual could have severe consequences for the reliability of the whole analysis.

Acknowledgements

We thank F.J. Chicano, F.G. Vilches, J.M. Giral and M. Anjos for help in the field, the personnel of the Reserva Biológica de Doñana for logistical help and accommodation and Microwave Telemetry for technical support. We thank M. Whittingham, J. Wilson and two anonymous refer-

ees for constructive comments on a previous draft of the manuscript. The study received funding by Natural Research Ltd, The Spanish Severo Ochoa Program for Excellence (SEV-2012-0262) and research projects CGL2008-01781, CGL2011-28103 and CGL2012-32544 of the Spanish Ministry of Science and Innovation/Economy and Competitiveness and FEDER funds, 511/2012 of the Spanish Ministry of Agriculture, Food and the Environment (Autonomous Organism of National Parks), JA-58 of the Consejería de Medio Ambiente de la Junta de Andalucía and by the Excellence Projects RNM 1790, RNM 3822 and RNM 7307 of the Junta de Andalucía. J.B. was supported by a Ramón y Cajal contract from the CSIC.

Data accessibility

Metadata on vital rates, social dominance, provisioning and nestlings' biomass available from the Figshare Digital Repository doi:10.6084/m9.figshare.1491385 (Sergio *et al.* 2015).

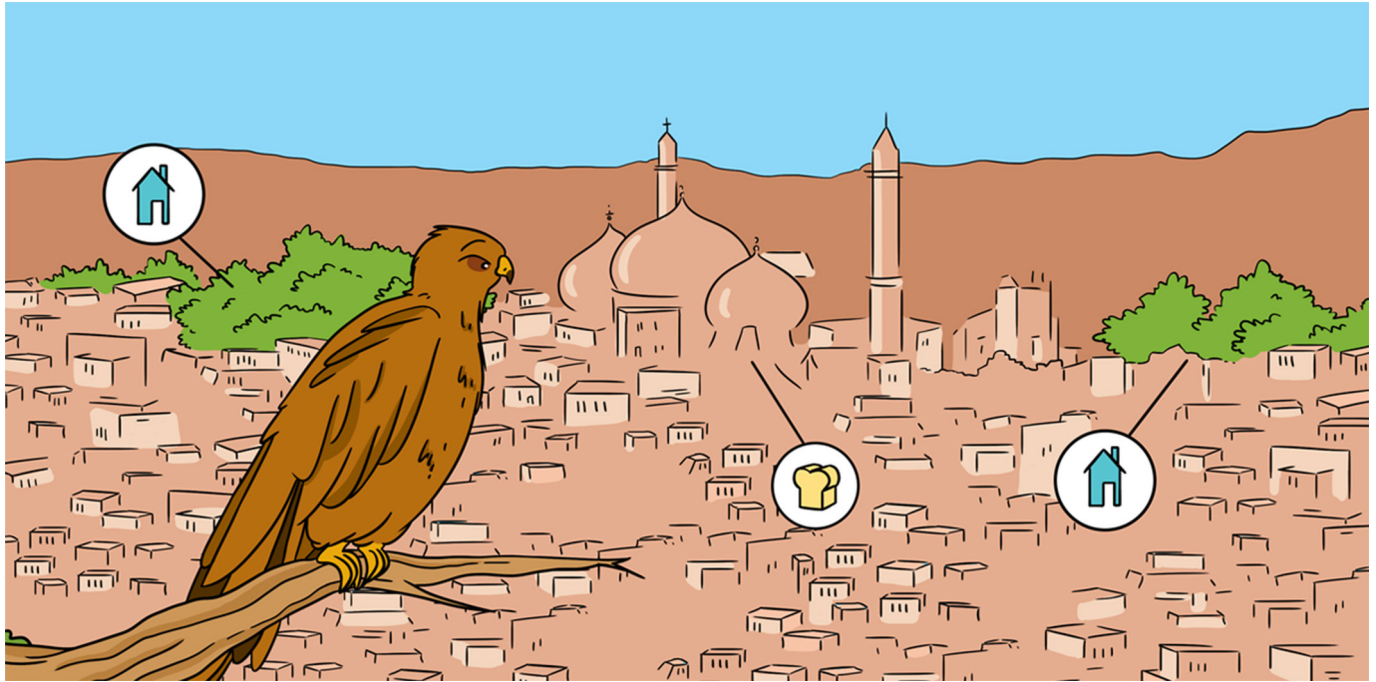
References

- Barron, D.G., Brawn, J.D. & Weatherhead, P.J. (2010) Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution*, **1**, 180–187.
- Blas, J., Sergio, F. & Hiraldo, F. (2009) Age-related reproduction in a long-lived raptor: a cross-sectional and longitudinal study. *Ecography*, **32**, 647–657.
- Bortolotti, G.R., Marchant, T.A., Blas, J. & German, T. (2008) Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. *Functional Ecology*, **22**, 494–500.
- Burnham, K.K. & Newton, I. (2011) Seasonal movements of Gyrfalcons *Falco rusticolus* include extensive periods at sea. *Ibis*, **153**, 468–484.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. (1987). *Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture*. Am. Fish. Soc. Monogr. No. 5., Bethesda, MD.
- Calvo, B. & Furness, R.W. (1992) A review of the use and the effects of marks and devices on birds. *Ring and Migration*, **13**, 129–151.
- Casper, R.M. (2009) Guidelines for the instrumentation of wild birds and mammals. *Animal Behaviour*, **78**, 1477–1483.
- Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G. & Butler, P.J. (2004) Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution*, **19**, 334–343.
- Crawley, M.J. (2007) *The R Book*. Wiley Press, Chichester.
- Croxall, J.P., Silk, J.R.D., Phillips, R.A., Afanasyev, V. & Briggs, D.R. (2005) Global circumnavigations: tracking year-round ranges of non-breeding albatrosses. *Science*, **307**, 249–250.
- Dodge, S., Bohrer, G., Bildstein, K., Davidson, S.C., Weinzierl, R., Bechard, M.J. *et al.* (2014) Environmental drivers of variability in the movement ecology of turkey vultures (*Cathartes aura*) in North and South America. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **369**, 20130195 1471–2970.
- Ferguson-Lees, J. & Christie, D.A. (2001) *Raptors of the World*. Houghton Mifflin Company, New York, NY.
- Foster, C.C., Forsman, E.D., Meslow, E.C., Miller, G.S., Reid, J.A., Wagner, F.F., Carey, A.B. & Lint, J.B. (1992) Survival and reproduction of radio-marked adult spotted owls. *Journal of Wildlife Management*, **56**, 91–95.
- Gervais, J.A., Catlin, D.H., Chelgren, N.D. & Rosenberg, D.K. (2006) Radiotransmitter mount type affects burrowing owl survival. *Journal of Wildlife Management*, **70**, 872–876.
- Godfray, J.D. & Bryant, D.M. (2003) Effects of radio transmitters: review of recent radio-tracking studies. *Science for Conservation*, **214**, 83–95.
- Gregory, M.J.P., Gordon, A.G. & Moss, R. (2003) Impact of nest-trapping and radio-tagging on breeding Golden Eagles *Aquila chrysaetos* in Argyll, Scotland. *Ibis*, **145**, 113–119.
- Kenward, R.E. (2001) *A Manual for Wildlife Radio Tagging*. Academic Press, London.
- Klaassen, R.H.G., Hake, M., Strandberg, R., Koks, B.J., Trierweiler, C., Exo, K.-M., Barlein, F. & Alerstam, T. (2013) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology*, **83**, 176–184.
- López-Jiménez, L., Blas, J., Tanferna, A., Cabezas, S., Marchant, T.A., Hiraldo, F. & Sergio, F. (2015) Ambient temperature, body condition

- and sibling rivalry explain feather corticosterone levels in developing black kites. *Functional Ecology* doi: 10.1111/1365-2435.12539.
- Marzluff, J.M., Vekasy, M.S., Kochert, M.N. & Steenhof, K. (1997) Productivity of Golden Eagles wearing backpack radiotransmitters. *The Journal of Raptor Research*, **31**, 223–227.
- McGrady, M.L., Ueta, M., Potapov, E., Uteckhina, I., Masterov, V., Ladyguine, A. *et al.* (2003) Movements by juvenile and immature Steller's Sea Eagles *Haliaeetus pelagicus* tracked by satellite. *Ibis*, **145**, 318–328.
- Murray, D.L. & Fuller, M.R. (2000) A critical review of the effects of marking on the biology of vertebrates. *Research Techniques in Animal Ecology* (eds L. Boitani & T.K. Fuller), pp. 15–64. Columbia University Press, New York, NY.
- Newton, I. (2008) *The Migration Ecology of Birds*. Academic Press, London.
- Paton, P.W.C., Zabel, C.J., Neal, D.L., Steger, G.N., Tilghman, N.G. & Noon, B.R. (1991) Effects of radio tags on spotted owls. *Journal of Wildlife Management*, **55**, 617–622.
- Peniche, G., Vaughan-Higgins, R., Carter, I., Pocknell, A., Simpson, D. & Sainsbury, A. (2011) Long-term health effects of harness-mounted radio transmitters in red kites (*Milvus milvus*) in England. *The Veterinary Record*, **169**, 311.
- Phillips, R.A., Xavier, J.C. & Croxall, J.-P. (2003) Effects of satellite transmitters on albatrosses and petrels. *The Auk*, **120**, 1082–1090.
- R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. URL <http://www.R-project.org>.
- Reynolds, R.T., White, G.C., Joy, S.M. & Mannan, R.W. (2004) Effects of radiotransmitters on northern goshawks: do tailmounts lower survival of breeding males? *Journal of Wildlife Management*, **68**, 25–32.
- Rodríguez, A., Negro, J.J., Fox, J.V. & Afanasyev, V. (2009) Effects of geolocator attachments on breeding parameters of Lesser Kestrels. *Journal of Field Ornithology*, **80**, 399–407.
- Rutz, C. & Hays, G.C. (2009) New frontiers in biologging science. *Biological Letters*, **5**, 289–292.
- Sergio, F., Blas, J. & Hiraldo, F. (2009a) Predictors of floater status in a long-lived bird: a cross-sectional and longitudinal test of hypotheses. *Journal of Animal Ecology*, **78**, 109–118.
- Sergio, F., Blas, J., Forero, M.G., Donazar, J.A. & Hiraldo, F. (2007a) Size-related advantages for reproduction in a slightly dimorphic raptor: opposite trends between the sexes. *Ethology*, **113**, 1141–1150.
- Sergio, F., Blas, J., Forero, M.G., Donazar, J.A. & Hiraldo, F. (2007b) Sequential settlement and despotic site-dependence in a migratory raptor. *Behavioral Ecology*, **18**, 811–821.
- Sergio, F., Blas, J., Baos, R., Forero, M.G., Donazar, J.A. & Hiraldo, F. (2009b) Short and long-term consequences of individual and territory quality in a diurnal raptor. *Oecologia*, **160**, 507–514.
- Sergio, F., Tavecchia, G., Blas, J., López, L., Tanferna, A. & Hiraldo, F. (2011a) Age-structured vital rates in a long-lived raptor: implications for population growth. *Basic and Applied Ecology*, **12**, 107–115.
- Sergio, F., Blas, J., Blanco, G., Tanferna, A., López, L., Lemus, J. & Hiraldo, F. (2011b) Raptor nest decorations are a reliable threat against conspecifics. *Science*, **331**, 327–330.
- Sergio, F., Blas, J., López, L., Tanferna, A., Díaz-Delgado, R., Donazar, J.A. & Hiraldo, F. (2011c) Coping with uncertainty: breeding adjustments to an unpredictable environment in an opportunistic raptor. *Oecologia*, **166**, 79–90.
- Sergio, F., Tanferna, A., De Stephanis, R., López Jiménez, L., Blas, J., Tavecchia, G., Preatoni, D. & Hiraldo, F. (2014) Individual improvements and selective mortality shape lifelong migratory performance. *Nature*, **515**, 410–413.
- Sergio, F., Tavecchia, G., Tanferna, A., López Jiménez, L., Blas, J., De Stephanis, R., Marchant, T.A., Kumar, N. & Hiraldo, F. (2015) Data from: No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. *Figshare*, <http://dx.doi.org/10.6084/m9.figshare.1491385>.
- Steenhof, K., Bates, K., Fuller, M.R., Kochert, M.N., McKinley, J.O. & Lukacs, P.M. (2006) Effects of radiomarking on prairie falcons: attachment failures provide insight about survival. *Wildlife Society Bulletin*, **34**, 116–126.
- Sunde, P. (2006) Effects of backpack radio tags on tawny owls. *Journal of Wildlife Management*, **70**, 594–599.
- Therrien, J.-F., Gauthier, G. & Bêty, J. (2012) Survival and reproduction of adult snowy owls tracked by satellite. *Journal of Wildlife Management*, **76**, 1562–1567.
- Vekasy, M.S., Marzluff, J.M., Kochert, M.N., Lehman, R.N. & Steenhof, K. (1996) Influence of radio-transmitters on Prairie Falcons. *Journal of Field Ornithology*, **67**, 680–690.
- Viñuela, J. (2000) Opposing selective pressures on hatching asynchrony: egg viability, brood reduction and nestling growth. *Behavioral Ecology and Sociobiology*, **48**, 333–343.
- Viñuela, J. & Bustamante, J. (1992) Effect of growth and hatching asynchrony on the fledging age of Black and Red kites. *The Auk*, **109**, 748–757.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**(Supplement), 120–138.
- Wikelski, M., Kays, R.W., Kasdin, N.J., Thorup, K., Smith, J.A. & Swenson, G.W. (2007) Going wild: what a global small-animal tracking system could do for experimental biologists. *Journal of Experimental Biology*, **210**, 181–186.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, NY.

Received 4 December 2014; accepted 29 July 2015

Handling Editor: Jeremy Wilson



CITIES: HOW DO SOME BIRDS THRIVE THERE?

Nishant Kumar^{1,2,3*}, Urvi Gupta², Yadvendradev V. Jhala², Qamar Qureshi⁴, Andrew G. Gosler^{1,3,5} and Fabrizio Sergio⁶

¹Department of Zoology, Edward Grey Institute of Field Ornithology, University of Oxford, Oxford, United Kingdom

²Department of Animal Ecology and Conservation Biology, Wildlife Institute of India, Dehradun, India

³Mansfield College, University of Oxford, Oxford, United Kingdom

⁴Department of Population Management, Capture & Rehabilitation, Wildlife Institute of India, Dehradun, India

⁵School of Anthropology and Museum Ethnography, Institute of Human Sciences, Oxford, United Kingdom

⁶Department of Conservation Biology, Estación Biológica de Doñana-CSIC, Sevilla, Spain

YOUNG REVIEWER:



LUANA

AGE: 14

Do you know that most humans now live in cities? This has caused a lot of trouble for many animal species. But a few opportunistic animals, like crows and pigeons that you commonly encounter in cities, benefit from dense human habitation. How does a very urbanized, paved, and populated landscape manage to support enormous flocks of birds in tropical cities? This is mostly unknown for urban birds like me: the Black Kite *Milvus migrans*. Researchers studying me in Delhi show that I depend on the food provided by humans and I prey on other common urban animals, such as pigeons and rats. The researchers of this article looked at the food that Muslims in the Indian subcontinent ritually offer kite birds and the impact these meat offerings have. Their analyses show that kite birds take cues from human activity, preferring densely populated areas in the city, with trees capable of holding a large nest, or

road configurations that allow for easy access to human waste and ritual food.

ABOUT ME

ECOSYSTEM

The functional units of nature, comprised of living organisms (plants, animals and microbes) in a particular area, in conjugation with the nonliving components of the interacting system.

VERTEBRATES

Animals with a spinal cord surrounded by cartilage or bone.

Do you know that many animal species take care of their young ones, much like humans? Humans have, however, singularly dominated the planet for thousands of years and more recently devastated most **ecosystems**. This is typically visible when looking at the steady increase of built-up spaces, such as cities. Within only a few centuries, humans have depleted (by weight) almost 99% of **vertebrates**, either through hunting or deforestation [1]. Despite this, there are a few animal species that take advantage of garbage-based food and their populations can also reach high numbers. Humans often see such urban exploiters as pests that occasionally cause trouble or damage properties.

I am one such species. Frequently misidentified as an “Eagle” by city-dwellers in India, kites successfully live alongside humans, opportunistically seeking the availability of food from human generated garbage. Kite birds are reported to be one of the most common and successful birds of prey in the world. Black Kites *Milvus migrans* (Figure 1) are found throughout Eurasia, Africa, and Australia. They almost exclusively live in villages, towns, and cities in India [2]. In Delhi, where kites primarily build their nests on trees, religious kite-feeding practices also provide food. Are you aware of the centuries-old religious Islamic practice of feeding meat scraps to kites for blessings, and to seek relief from sins [3, 4] (follow the video link)? People of Islamic faith live in concentrated and well-defined areas of Delhi (hereafter “Muslim colonies”) (Figure 2). Researchers have shown that enormous food-subsidies may explain Delhi’s capacity to host so many urban animals [2].

I must stress that there are very few studies that focus on the impact of increasingly built-up spaces in previously non-human populated tropical regions. Most of this urban change is taking place closer to the equator [5]. Animals that are found in these cities play an important role in people’s sense of connection with nature. They also remove tons of decaying garbage from the streets and provide a vital sanitary service for humans. One way to address the lack of knowledge on animals that live in cities and villages is researching their choice of suitable living areas and how human activities make cities a useful habitat for animal species. A group of researchers led by Nishant Kumar studied how a parent kite pair identified an urban space in Delhi to live in.

WHAT DO RESEARCHERS EXAMINE WHEN STUDYING A COMMON URBAN BIRD?

What prompted these researchers to study the ecological aspects of a common species? Citizens often assume “obvious roles” for

Figure 1

(A) An urban Black Kite *Milvus migrans govinda* breeder with a twig in its beak is an opportunistic predator that capitalizes on human food subsidies. Photo Credit: F Sergio. We fixed GPS platform terminal transmitters on a few breeding kites to understand their movement with respect to the distribution of food resources. Photo Credit: U Gupta. (B) A view from a Black Kite nest on a telephone-tower in Delhi. A heterogeneously developed city needs a multitude of strategies for opportunistic acquisition of urban resources. These strategies are fine-tuned, collectively, on local habitat structure and human activities that provide edible-waste and site-specific ritualized meat feeding. Photo Credit: L Narayan.

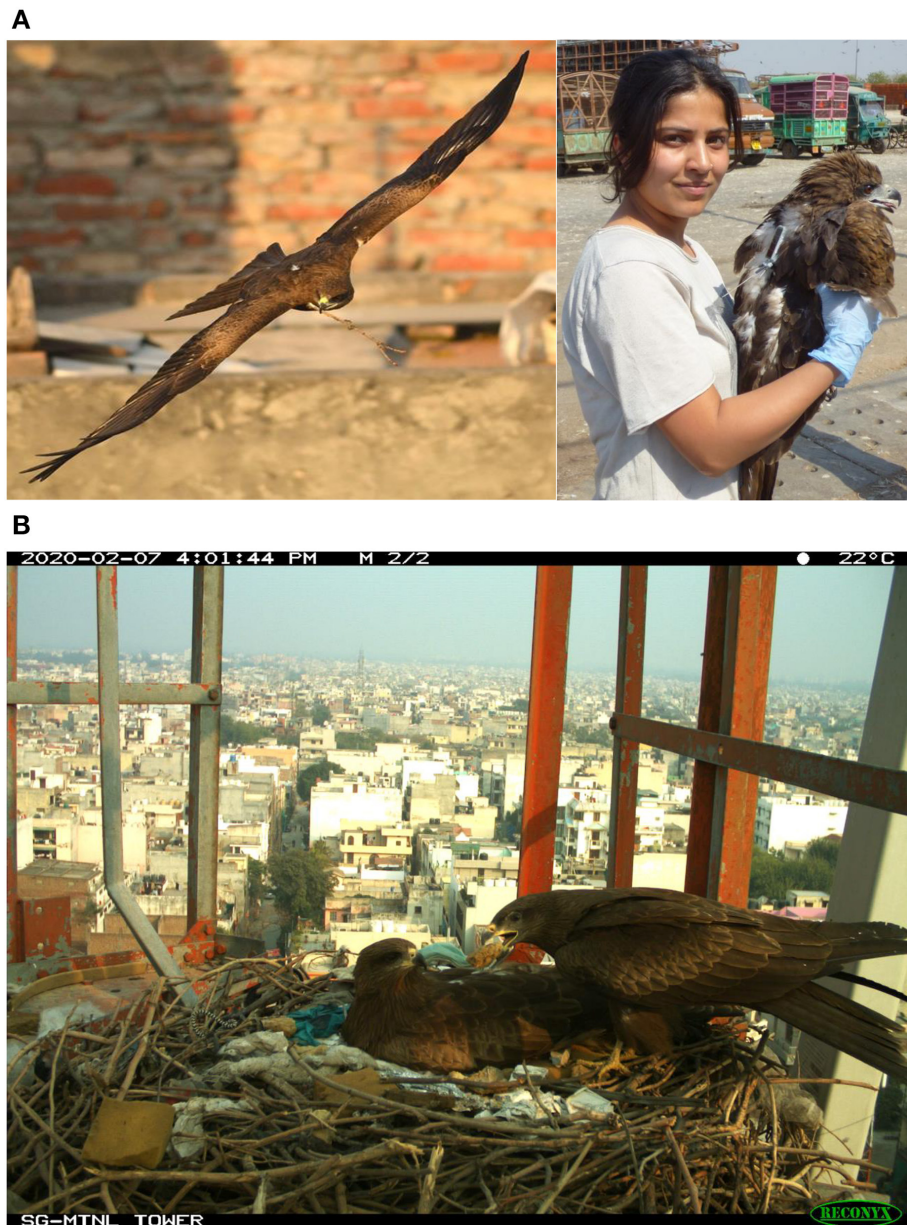


Figure 1

RAPTOR

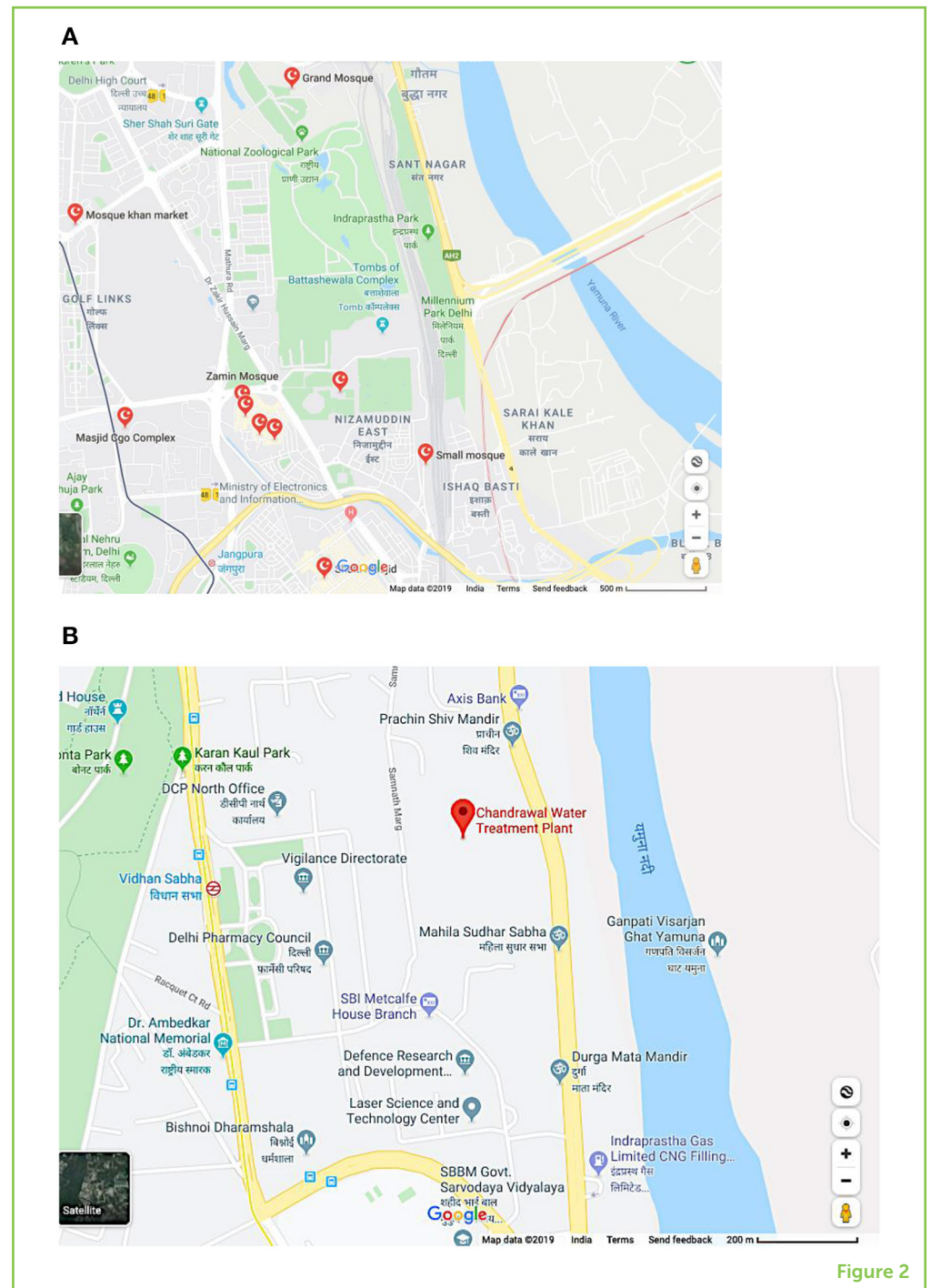
Birds of prey.

urban species, based on occasional observations or common sense. Interestingly, for the citizens of Delhi, and even for Kumar himself, the idea that a (large) **raptor** could nest in huge numbers within a city was unimaginable. Kumar's initial idea of a raptor was a fierce eagle that breeds in some remote, pristine forest, in small numbers, much like tigers. But reality often challenges human simplifications, and this speaks volumes about the wonders and actual machinery of nature waiting to be unraveled.

Once the team noticed sharp variations in the density of kite-nests, they systematically studied the number and productivity of nests between 2013 and 2016 at 24 sampling-plots, each of 100 hectares. These plots covered most of the possible urban settings within Delhi,

Figure 2

Schematic depiction of the major difference between the spatial proximity of mosques (depicted in red, with Islamic symbol) to (A) a sampling unit, the National Zoological Park, and (B) a random location chosen by the computer in Delhi. Black Kites *Milvus migrans* capitalize on ritual meat tossing near mosques which were less likely to be found in the vicinity of a random location, implying their importance for kites' habitat preferences. Credit: Google Maps.

**Figure 2**

from semi-natural to extremely built-up sites. This resulted in a sample of 154 nests, checked every 7–10 days until they had chicks of at least 45 days, i.e., ready to fly and become fledglings. For each nest, the effort provided data on the number of young birds that were successfully raised until the flight-stage.

Now, considering that parent kites strategically choose a nesting-site, one would expect successful breeding-investment. Logically, such a strategy should simultaneously take into consideration the proximity

VARIABLE

An attribute that describes a person, place, thing, or idea.

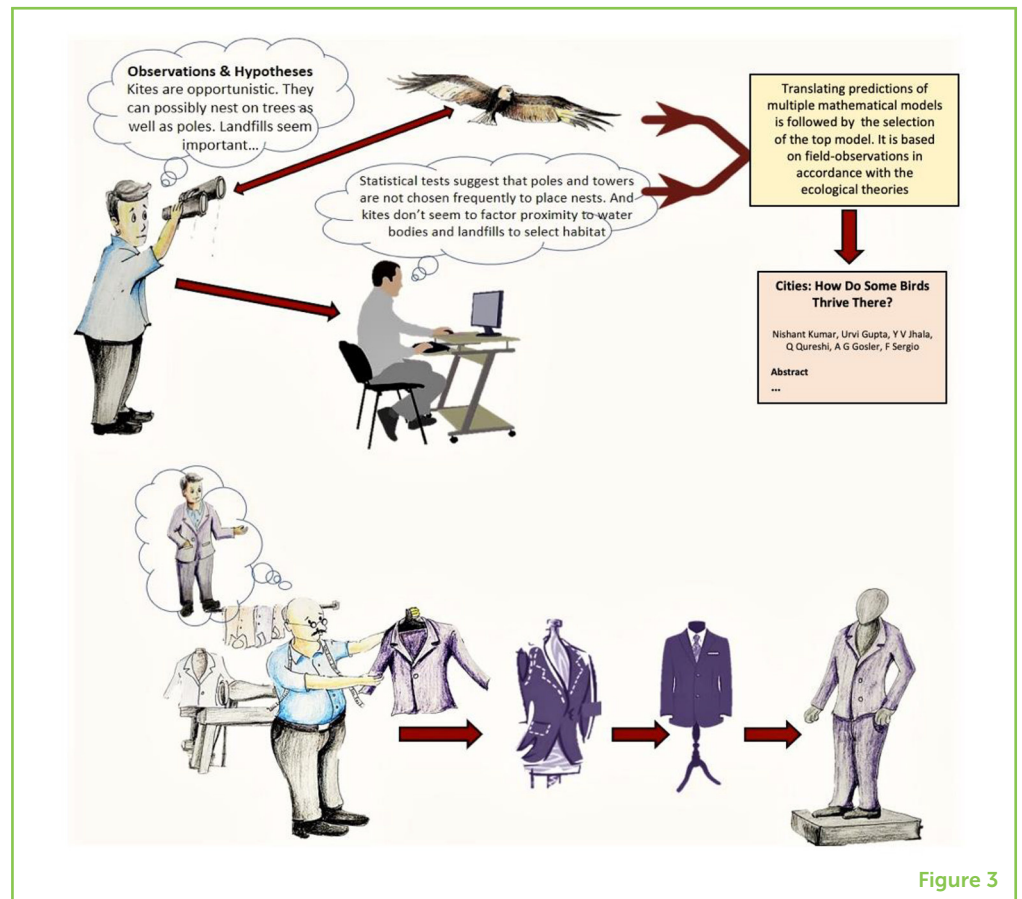
to reliable food sources and safety from potential predators and harsh weather. Researchers had to imagine what a city would look like to me from various altitudes, much like the outer view during the takeoff or landing of an airplane. Quite similarly, while flying at different heights, birds notice and choose from apparent features of a landscape. Researchers also considered **variables** to represent human socio-cultural activities, such as the religious ceremonies that provide kites with food and other resources.

In particular, researchers understood my nesting-habitat selection criteria within different developed pockets of a megacity. A typical way to determine such selection criteria is a comparison of actual nest locations (154) within the 24 sampling study plots, with a matching number of locations randomly chosen by a computer program (ArcGIS, a computer program for geographic analysis, i.e., a Geographic Information System, also called a GIS). At each computer-generated random-location, researchers selected the nearest tree or tower judged capable of supporting a kite nest. Logically, researchers expected kites to be choosy and thus they expected the site-based properties considered important for kites to differ significantly between actual nest locations and computer-generated random-locations. Researchers were additionally helped by remotely available data from a few kites that were carrying GPS-transmitters (transmitters that, once placed on a bird, record its location every few minutes, just as your mobile phone does) and confirming site-based properties important for kites, such as a circular area made up of a 500 m radius, frequently explored around the nest (called a "breeding territory") (Figure 1A). Kites regularly visited ritual feeding sites near mosques with very deliberate, directed journeys.

The site-based properties that allowed for comparisons of nest-locations with random points were primarily of three types: (a) at or around the nest level, e.g., the tree species and height, area of the woodlot around the nest, intensity of human street use around the nest, and the proximity to water and a waste dump, (b) within 500 m radial area around each nest and random site, such as the urban architecture or extent of tree cover and the built-up space, local density of buildings or roads, and (c) at each nest and random location, they also collected representative spatial data for ritual feeding activities, such as the proximity to large Muslim colonies. Further, at each nest or random location, the focal tree's situation with respect to surrounding trees was defined important in the following increasing order: an isolated nesting tree < in a linear roadside avenue plantation < within a park or woodlot. Researchers also classified the nests or random locations in two categories, depending on a high or low amount of edible food-waste (Figure 2).

Figure 3

A broad analogy can be found in the work of a readymade garment tailor and a field-researcher who starts a new research on a species. Both use models to test the fit: a tailor uses wooden-models to stitch clothes of various sizes, while a researcher uses mathematical-models that help them choose from the set of propositions (hypotheses) about the ecological criteria, as observed in the field. Sketch credit: Poonam Pal.



HOW DO RESEARCHERS INVESTIGATE MY PREFERENCES?

You must have observed clothed, human-like mannequins in clothing stores. Do you know that regular tailors stitch clothes for unknown buyers? They actually make use of similar “wooden-models” of various size categories (small, large, extra-large, etc., Figure 3) to stitch garments. Much like the tailor who stitched the readymade shirt you are wearing, a researcher who begins an ecological study is unaware of the preference criteria of non-human organisms. Considering that humans cannot look into my (kite) mind, field-researchers make meticulous observations to prepare a set of guiding propositions called **hypothesis** with respect to kite activities (Figures 1, 2). Subsequently, using data, they test the validity of these propositions using statistical programs and various “mathematical models” which are expected to best reflect my urban ecology. Ultimately, the research team arrives at the simplest final model that adheres well with the real, on-field observations on kites. Researchers validate such models using mathematical **algorithms** to reflect bird choices. Models inform why certain urban choices by the experienced and dominant breeding-kites make them more successful parents (Figure 3).

HYPOTHESIS

A suggestive idea to explain phenomena under observation.

ALGORITHM

A set of rules that must be followed when solving a particular problem.

BROODING/ INCUBATION

Acts of sitting on eggs or chicks by the female bird to maintain uniform heat and humidity.

ADAPTIVE/ ADAPTATION

An evolutionary process where populations of a species become better suited to their habitat.

WHY DO KUMAR AND COLLEAGUES' MATHEMATICAL MODELS STAY JUSTIFIED?

Living in cities is a challenge for non-humans. Most of us kites build nests on trees, but not all trees have kite nests on them. This is because we “choose” to live in certain habitats. During **incubation** and initial **brooding**, the female kite is restricted to the nest for about 2 months. During this time the male takes charge of feeding the whole family. Researchers found that we avoided areas in the city that are contiguously built-up. We are more likely to identify nesting-habitat in safe clusters of trees in a park or woodlot that allow easy access to food coming from garbage piled informally on roadsides, and ritual offerings of meat within densely populated Muslim colonies. In addition, those among us that could breed in the areas with a greater extent of tree-cover in proximity to the sites of ritual feeding managed to raise more young-kites. We would, of course, like to identify habitable patches that are simultaneously associated with ample tree cover near multiple, large Muslim colonies. Thus, researchers defined this strategy of exploiting food near humans to be **adaptive/adaptation**, considering it was associated with higher nesting-success. The simplest and most-accurate mathematical model was based on 4 years of data, and observant-researchers (Figures 2, 3). In a way, the variation of food availability across the city was uniquely tied to complex human themes, which included (1) the complex history of *Muslims* in India; (2) planning of refuse disposal and urban-constructions useful for kites; and (3) cultural and religious practices.

People have an innate love for living creatures called Biophilia (bios: living; philia: love of) that is further diversified by religious beliefs in South Asia, where animals are considered as God's vehicles, or messengers from God. Like any megacity, Delhi will witness rapid change in the coming decades in terms of structure, management, and culture [4, 6]. Kumar and his colleagues have noticed the poor prevalence of the meat offering practice in youngsters, a generational shift that will eventually alter cultural tolerance for backyard-biodiversity [3]. In particular, our dependency on ritual feeding could be seen as a local uniqueness that connects citizens with nature and is thus vital research that should actively be promoted.

AUTHOR CONTRIBUTIONS

NK and UG led the writing of the first draft. All authors contributed to aspects of preparation and writing of the paper and approved the final version.

ACKNOWLEDGMENTS

We thank Dr Becky Thomas, Ester Dias, Hedwig, the anonymous mentor and Luana for constructive comments that greatly improved the manuscript, and Ujjwal Kumar and the Director, Dean and Research Coordinator of the Wildlife Institute of India for materials, encouragement and advice on various aspects of the project. The authors are grateful to the FCO Chevening - HSBC Scholarship, Hansell Travel Grant and Discretionary Grant from Somerville College (Oxford), Dissertation grant of SoGE, the Raptor Research and Conservation Foundation (Mumbai), the Government of India's Ministry of Environment, Forest and Climate Change, and the University of Oxford (Felix Scholarship Trust) for funding. Delhi Police, the Forest Departments of Delhi and Uttar Pradesh, and the municipal corporations and civic bodies of the Government of NCT, Delhi, helped with legal permits. Members of the "Black Kite Project Group," especially Laxmi Narayan, Prince Kumar, Poonam, Zehen, Ameer, Yukti, A Singh, P Kumar, H Malhotra, and G Singh helped in the fieldwork. Delhites extended enthusiastic participation and support, along with the important insights.

REFERENCES

1. Smil, V. 2013. *Harvesting the Biosphere: What We Have Taken From Nature*. Cambridge, MA: MIT Press.
2. Galushin, V. M. 1971. A huge urban population of birds of prey in Delhi India. *Ibis* 113:522. doi: 10.1111/j.1474-919X.1971.tb05189.x
3. Kumar, N., Gupta, U., Jhala, Y. V., Qureshi, Q., Gosler, A. G., and 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.* 21:339–49. doi: 10.1007/s11252-017-0716-8
4. 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 (Bristol: Equinox Publishing Ltd). p. 108–21.
5. Anonymous. 2016. Rise of the city. *Science* 352:906–7. doi: 10.1126/science.352.6288.906
6. Sharan, A. 2014. *In the City, Out of Place: Nuisance, Pollution, and Dwelling in Delhi, c. 1850–2000*. Oxford: Oxford University Press.

SUBMITTED: 23 July 2019; **ACCEPTED:** 25 March 2020;

PUBLISHED ONLINE: 22 April 2020.

EDITED BY: Becky Louise Thomas, University of London, United Kingdom

CITATION: Kumar N, Gupta U, Jhala YV, Qureshi Q, Gosler AG and Sergio F (2020) Cities: How Do Some Birds Thrive There? *Front. Young Minds* 8:46. doi: 10.3389/frym.2020.00046

CONFLICT OF INTEREST: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

COPYRIGHT © 2020 Kumar, Gupta, Jhala, Qureshi, Gosler and Sergio. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

YOUNG REVIEWER

LUANA, AGE: 14

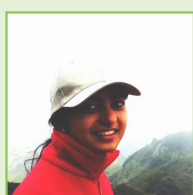
I like to roller skating, ride a bike, watch movies, and hang out with my friends.



AUTHORS

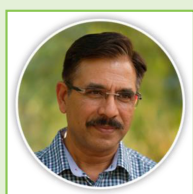
NISHANT KUMAR

Nishant is a researcher jointly based at the Department of Zoology (University of Oxford) and the Wildlife Institute of India. In Delhi, he tries to understand opportunistic animal responses to resources provided by humans, and how centuries of coexistence have tied urban ecology of commensals with religiously founded patronage and ritual animal feeding by people. He is currently interested in understanding the socio-economic impacts of scavenging ecosystem services provided by opportunistic commensals and how their biocultural links are vital for a sustainable urban future in South Asia. *nishant.kumar@zoo.ox.ac.uk; ryu.nishant@gmail.com



URVI GUPTA

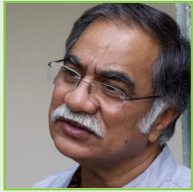
A wildlife enthusiast since childhood, Urvi is the Project Biologist at the Wildlife Institute of India and leads the Black Kite Project. A traveler who likes to see new places, nature-reserves and cultures, Urvi has always been an environmentalist, exemplifying carpooling, waste reduction and minimalism to influence family and friends to live sustainably. Having a background in Zoology from Delhi University and a Masters in Biodiversity, Conservation and Management from Oxford as a Chevening Scholar, she hopes to bridge the gaps between disciplines for wildlife conservation. She is interested in conservation, evolutionary ecology, human-animal interactions and science communication.



YADVENDRADEV V. JHALA

Yadvendra Dev is a carnivore biologist based at the Wildlife Institute of India. He has been passionate about animals and wilderness since his childhood and wanted to become a zookeeper. His current interest domain covers population ecology, behavioral ecology, and conservation biology and genetics. He leads multiple research programs on the predator-prey dynamics within the Indian protected area network, e.g., the tiger and its prey, and Asiatic Lions. He is also leading the Great

Indian Bustard conservation breeding program and is involved in the countrywide estimation and monitoring of the tiger and its prey species.



QAMAR QURESHI

At the Wildlife Institute of India, Qamar jointly leads the famed All India Tiger Monitoring Project with Yadvendradev. With expertise in landscape ecological methods, he has worked on habitat use patterns using remote sensing and GIS. He is currently involved with projects dealing with biodiversity assessment at the landscape levels. He leads the research on Gangetic Dolphin, working throughout rivers Ganges and Brahmaputra. He also works on rhesus macaques, blue bulls, and wild pigs to understand the human-animal interactions and conflicts. Besides wildlife research, Qamar is an avid reader with a wide taste that he considers essential for every science enthusiast.



ANDREW G. GOSLER

Andy researches questions in Ornithology and Ethno-ornithology concerning Nature Conservation in the broadest terms. He holds a joint position between the Zoology and Anthropology departments at the University of Oxford. He studied the Great Tit population of Wytham Woods and how finely tuned adaptations of the birds fitted them to their ecological community. This work has also contributed to environmental monitoring and conservation. His work now is focused on the significance of birds in engaging people with nature, both for their benefit and the benefit of wildlife, and helping people to understand how their dependence on nature means they must protect nature.



FABRIZIO SERGIO

A book gifted by his father, based on the tigers of Ranthambore National Park-India, catalyzed Fabrizio's childhood passion for wildlife. He is based at Doñana Biological Station-CSIC, Spain. He has researched several diurnal and nocturnal raptor species, with a special interest in species interactions, climate change and demography.



भारतीय वन्यजीव संस्थान
Wildlife Institute of India



Our Feathered Co-inhabitants of Delhi



Coexisting
migrant and resident Black Kite
races in a developing megacity

If you're a lay / city person, you probably know us as Eagles !

Worse, they call us Vultures,
crows, and even sparrows!
(Drunk, eh?)

Oh Yeah ! a janitor's worth
is established only on absence
from duty.
Poor Vultures ! [SIGH]

Birders know me as Lineatus.,
Call me Linn.



And I am Govinda! *Milvus migrans* govinda.

I'm all streaky, with more rufous coat,
Sporting yellow tarsi, you seem light and short!

Short goon I'm, O' Russian visitor,
I munch on feeding rituals, as a city scavenger.



Black-eared is what i am called,
with a white carpal patch.
While we feast on landfill offal
your adaptations have no match.

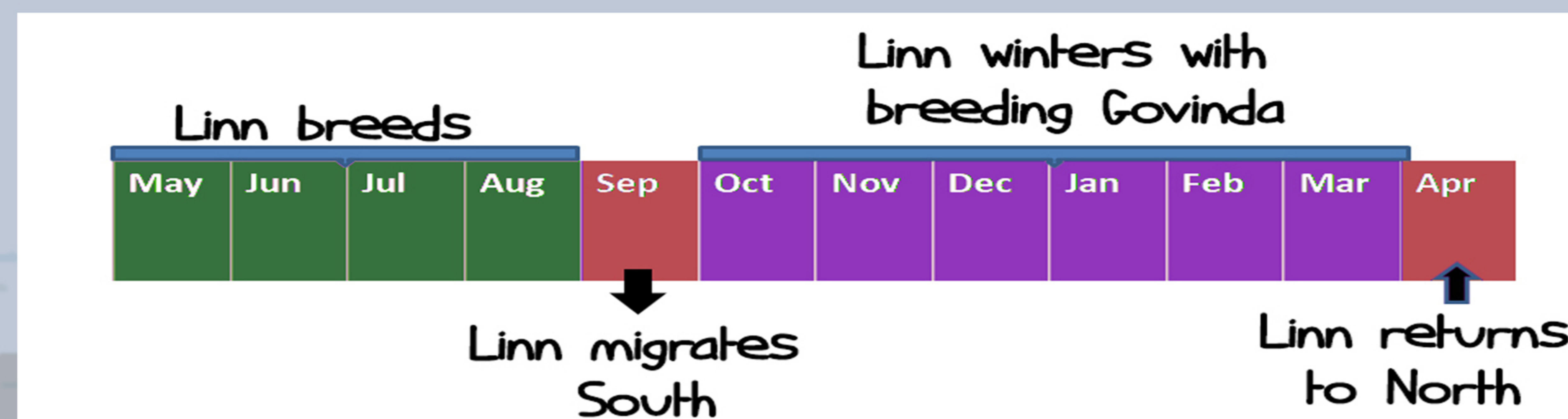
Hand-in glove with Indians,
religiously i evolved..
Share your story in elaboration,
when the reader is on hold.



Brrrrr....See there ! The pastoralists depart. Time to pack and leave for a winter vacation, folks !



Oh Yeah !!!



We have been doing "steeplechase" across Chinese highlands, deserts, and the mighty Trans-Himalayas, for millions of years, before you humans left Africa.



But in mere 300 Years, our favourite wintering grounds have been riddled by your enormous cities.

Too fast a change you see !



In the region you stand and read about us,
we annually meet our old cousins, the Govinda kites.

Evidently, these "architects" build cities
for their folks. As facultative scavengers,
we adaptively nest near them and
pretty much snatch morsels from their
hands.



Unassuming, as "immigrants"
we have
to suffice on
their predictable garbage and offal!

What all one goes through to
be a parent, post winter.

Hmm..., thankfully, Delhites (Muslims)
ritually offer us meat chunk
subsidies. We teem and nest in

their city parks and woodlots to capitalize, and yield to become
the commonest raptors.

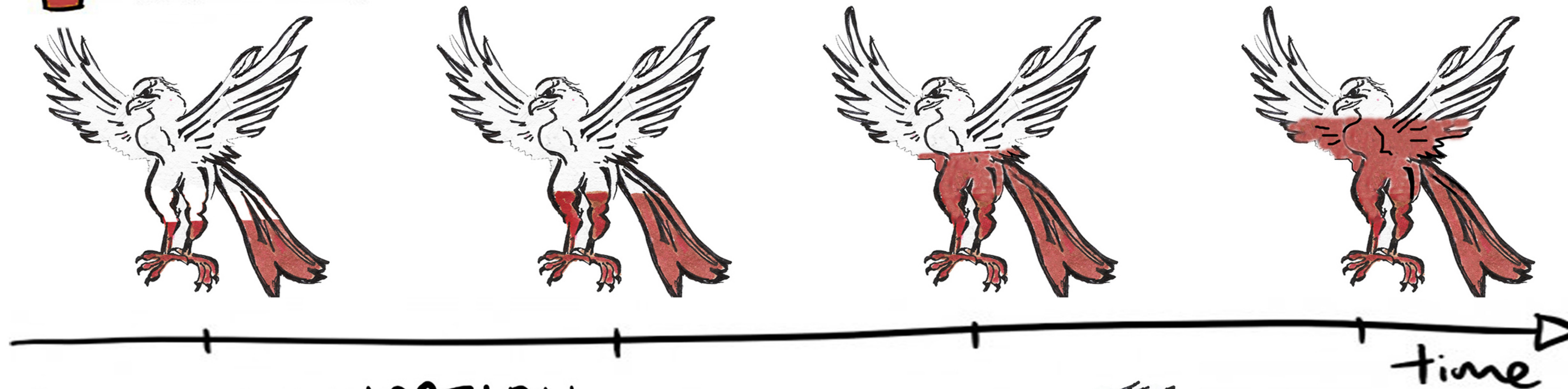




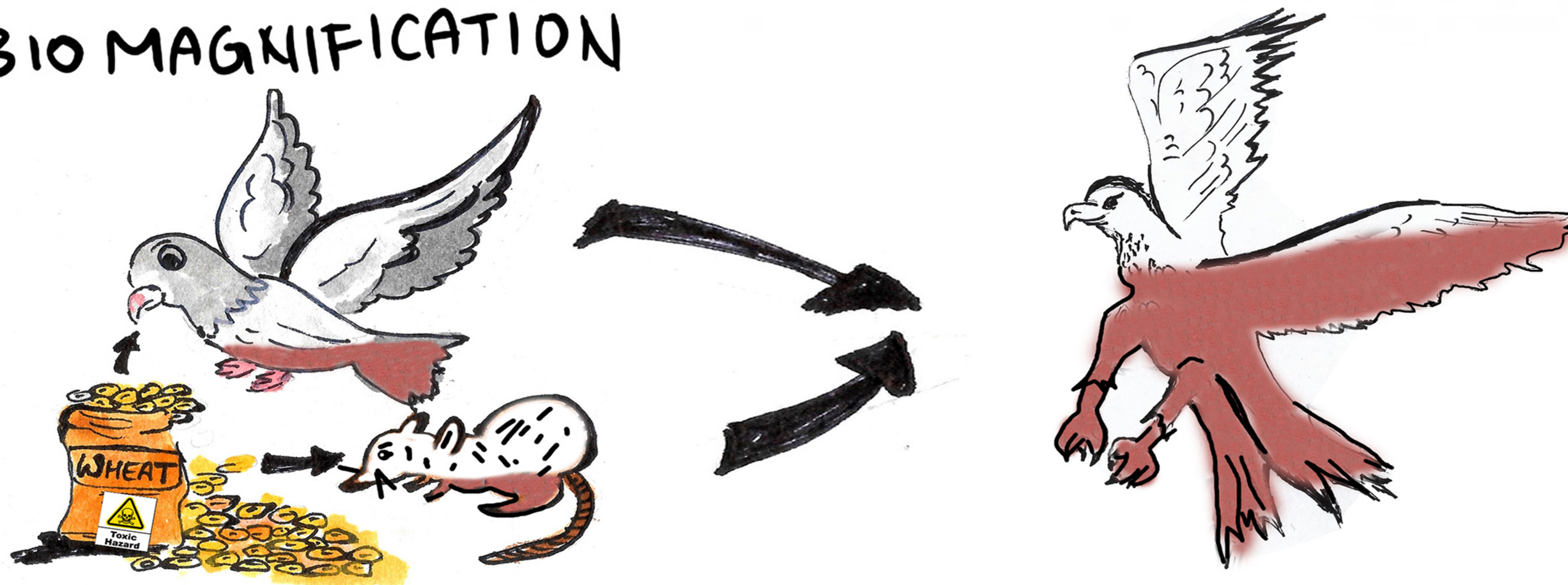
But as the saying goes, Nothing is Free ! We wonder about the consequences of their " urban fast food " : Toxic metals, bioaccumulation, etc. is what i read on Google.

BIOACCUMULATION

■ - contaminant



BIO MAGNIFICATION

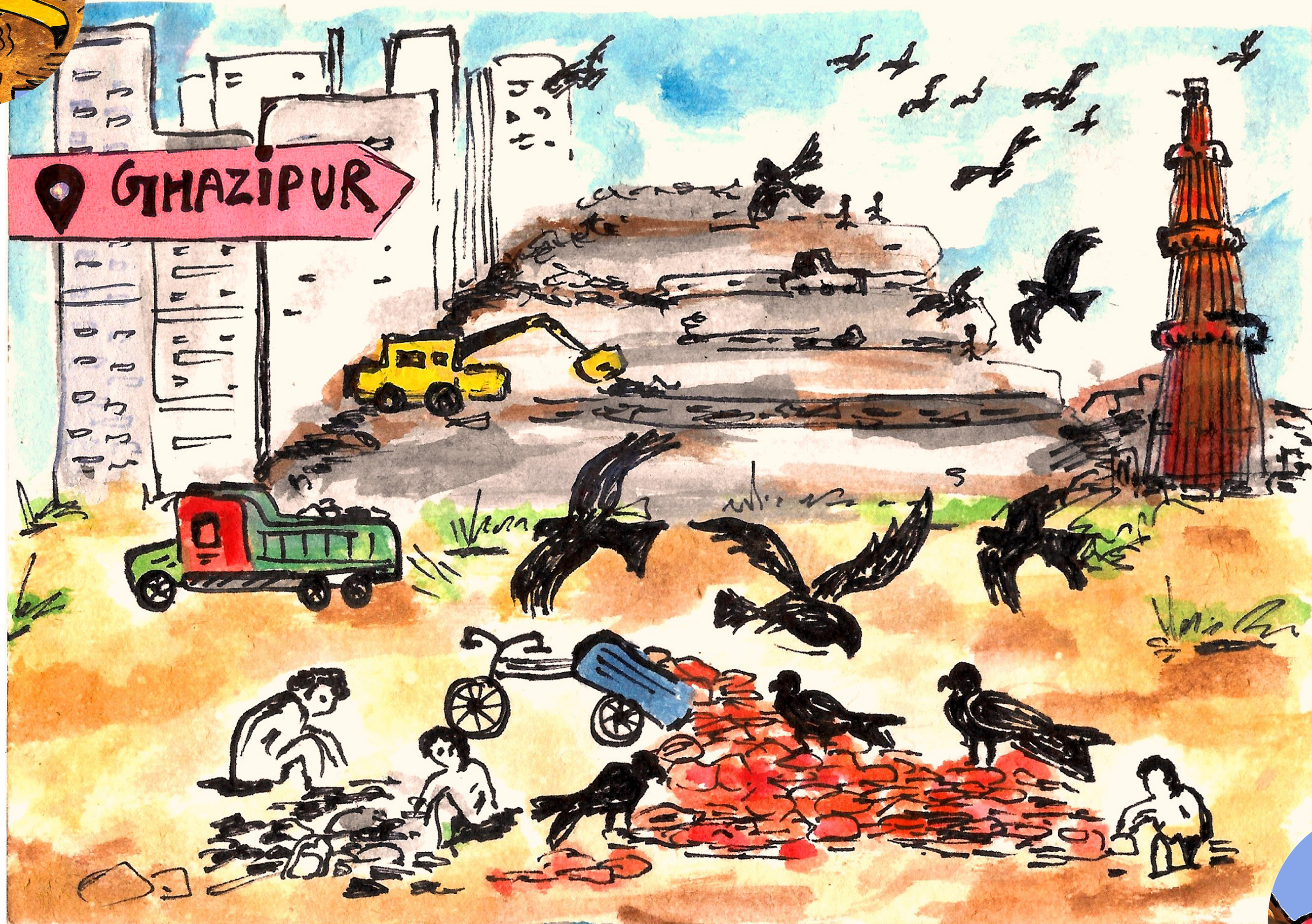


Yeah ! Our new neighbours, a lazy nesting couple : they lost their chicks to perpetual meat chunk diet. The pale appearance and bone deformities of chicks were scary.

Don't forget its consequence to our inner worlds : "the microbiome". Some of the readers would recall my range. It coincides with the hot spots of bird flu in China.



Add to it the expected preparedness for the months you guys are not here. Relentless garbage accumulation will only yield aircraft collisions, and higher likelihood of pathogen spillage.



You are right ! Homogeneity in cities physical structure, and social fabric will make my upcoming vacation rather boring.





Affirmative !
Unless the younger
generation picks the walking
boots to crusade against
extinction of experience,
we won't even find place in
their folklores.



Small Indian Kite
(*Milvus migrans govinda*)

©F. Sergio



Black-eared Kite
(*Milvus migrans lineatus*)

©L. Narayan

Google us @

1. Density, laying date, breeding success and diet of Black Kites *Milvus migrans govinda* in the city of Delhi (India).
2. Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools
3. Raptors associated with airports and aircraft. In the book: *Raptors in human landscapes: adaptations to built and cultivated environments*: Page # 315–323.
4. <https://delhikiteswixsite.com/121212>





You all can help !
Ask us @ : delhikiteswii@gmail.com
Follow us on Twitter : @delhikites

Acknowledgements

- Director, Dean and Research Co-ordinator, WII
- Forest Dept. Delhi And U.P. ; Delhi Zoo, Delhi Univ, Civic Bodies, Police and Citizens
- Black Kite Project Team , friends and well-wishers



©delhikites





भारतीय वन्यजीव संस्थान
Wildlife Institute of India



दिल्ली के सह-निवासी पक्षी



जानिए

अपनी निवासी व प्रवासी चीलों को

ईगल? पता नहीं ये 'सभ्य' शहरी हमें और किन-किन नामों से पुकारेंगे !

बिलकुल ! अब इन्हें गिद्ध याद आ रहे हैं ? प्रकृति के सफाई कर्मचारी आज की पीढ़ी के लिए "रामू काका" रह गए हैं । बेचारे गिद्ध !

अरे, हमें तो ये गिद्ध कौवा, गौरैया और न जाने किन किन नामों से बुलाते हैं P. K. है का ?



अंग्रेजी में मुझे lineatus कहते हैं ।
वैसे 'लिन' उपनाम कैसा रहेगा?

हाँ भाई, चीनी परिवेश का असर तोह पड़ेगा ही! लिन :)
मैं पूरा गंगा घाट वाला देसी, मिलवस मिर्गेंस गोविंदा हूँ।
हाव-भाव , चाल-ढाल, ओह गोविंदा !

धारीदार है तन मेरा, तुझसे गोरा रंग । पतली,
पीली सूखी टाँगे, तू छोटा- हल्का बेढंग ।

छोटा हूँ, पर बड़े काम का, सुन रूसी मेहमान ।
सड़ा-गला खाकर करता, सड़के साफ़ तमाम ।



काली कनपटी वाला मैं, पंख के
नीचे सफ़ेद । मैं भी कूड़ा जम
कर खाता, तू बता अब अपना
भेद ।

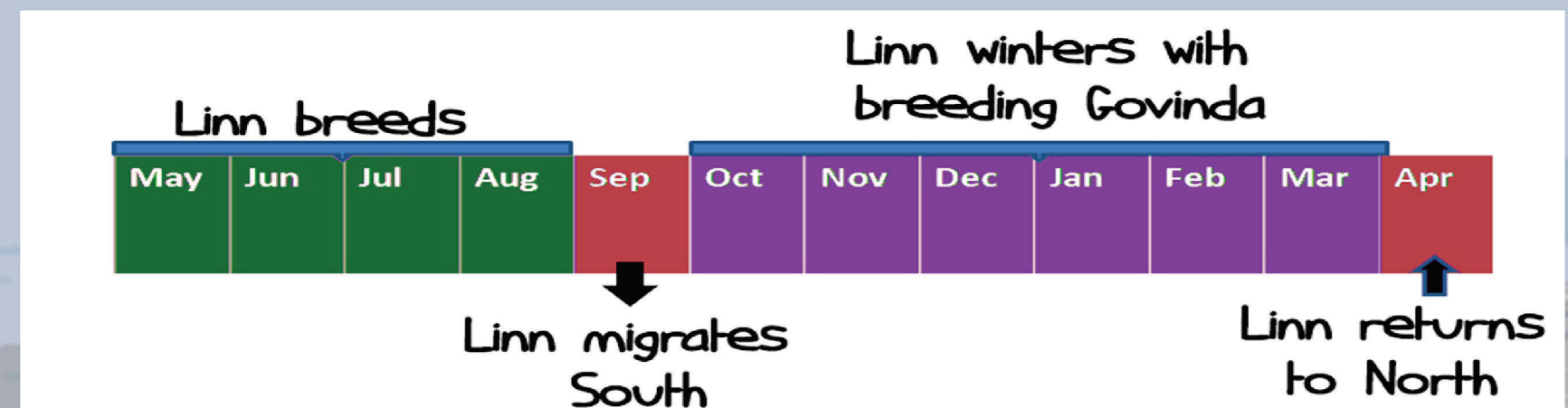
हाथ मिलाकर देसी लोगों से, बढ़ी है
मेरी शान । ध्यान खींच अपने पाठक
का, खुलकर बता अपनी पहचान ।



वो देखो, छोटे होते दिनों के साथ घुमंतु चरवाहे भी पलायन कर रहे हैं !
समय रहते दक्षिण निकल लेते हैं, वर्नाऊह हू हू... (ठंड) !



तो चलो!!



अरे, तुम इंसानों के पूर्वजों के अफ्रीका छोड़ने के लाखों साल पहले से हमारी उड़ान चीनी पहाड़ एवं रेगिस्तान और हिमालय की चोटियों को बौना करते आयी है।



हालांकि महज ३०० सालों के तुम्हारे शहरीकरण ने हमें पलायन के रास्ते में कई बार भटका दिया है। महज ३०० साल!



वैसे हम सालाना हज़ारों मील का सफर तय कर ६-७ महीने गोविंदा भाइयों के साथ बिताते हैं ।

भई, हम सभी तो इनके शहरों में पुरे ढल चुके हैं । कई बार तो हम मौकापरस्त, इनके हाथों से निवाला झपट ले जाते हैं ।



इनके लिए तो हम तुच्छ पक्षियों का एक झुण्ड है, जो कूड़े के ऊपर मंडराता है । इन्हें क्या खबर कि हम प्रवासी चीले यह सब मात्र बेहतर प्रजनन के लिए करती है ।



हाँ यार, पर पुरानी दिल्ली के बाशिन्दे हमें सदियों से गोश्त छिछड़े खिलाते आये हैं । इस्लाम में इसे चील का सद्क कहते हैं , यह मानते हुए कि हम

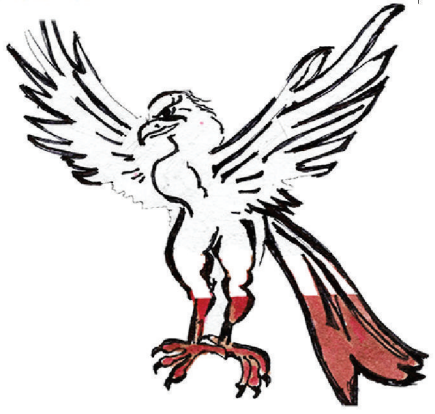
फ़रिश्ते उनकी दुआएं उपरवाले तक पहुंचा देंगे, या उनकी मुसीबतें दूर ले जाएंगे । जवाब में दिल्ली की चीलों के घोंसले इस परिचलन को इस्तेमाल करने की लिए बनते हैं ।



पर भई, मुफ्त का चन्दन कब तक घिस सकते हैं ? वो तो अच्छा है कि तुम भी हमारी तरह प्रजनन के समय आवश्यकतानुसार ताज़ा शिकार कर लेते हो | मैं तो बस इंसानी बस्तियों के कूड़े वाले लंगर को लेकर चिंतित हूँ | गूगल पर ऐसी मुफ्तखोरी के गंभीर परिणाम बताये गए हैं :- विषैली धातु, जैव-संचयन आदि |

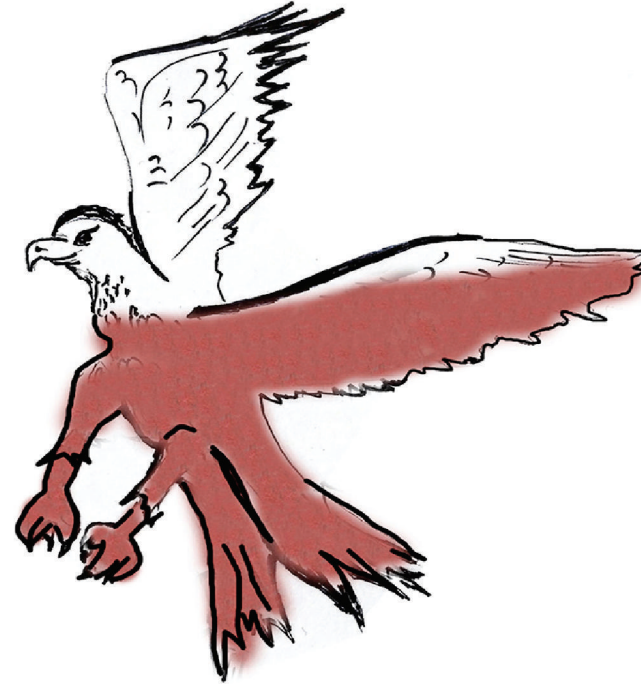
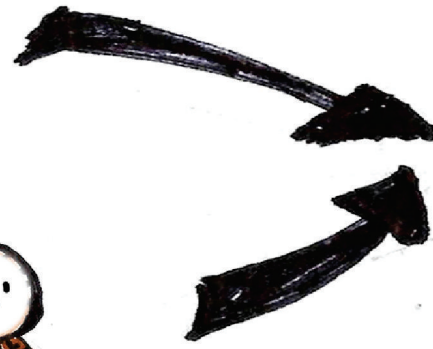
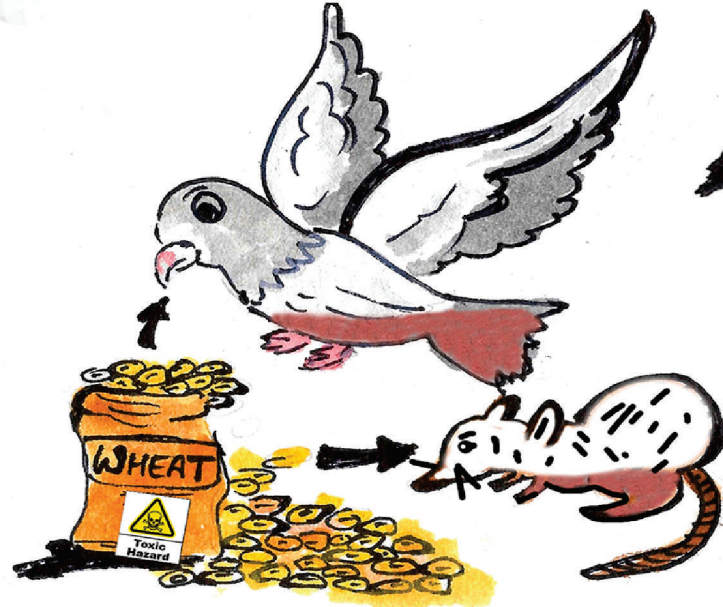
जैव-संचयन

■ - दूषित-पदार्थ



समय

जैव आवर्धन



यार तुम्हारी चिंता सौ टके ठीक है | अब हमारे पड़ोसी घोंसले वाले नए गोंविदा जोड़े को ही ले लो | छिछड़ों पर मुफ्तखोरी कि वजह से उनके बच्चे निकल लिए | कुपोषित, टेढ़ी हड्डियों देख कर दया आ रही थी |

और एक बात तो सभी भूल जाते हैं :- इस मुफ्तखोरी और शहरीकरण का हमारे सूक्ष्म-जैव विविधता पर क्या असर होगा | वैसे चीन में हमारी वितरण रेंज घातक बर्ड-फ्लू वाले इलाके से जुड़ी है |



कूड़े के पहाड़ बनाने वाले शहरियों को उन महीनों के लिए योजना बनानी चाहिए जब तुम सभी चले जाते हो | वस्तुतः कूड़े में लगातार वृद्धि से चील और हवाईजहाज़ का टकराव, और इंसान - चील के बीच बीमारीयों के अदान-प्रदान का खतरा है |



ठीक कहा भाई | इनके शहरो में प्रायः पाई जाने वाली एकरूपता मेरी ठंड की छुटियों को उबाऊ बना देती है |





एकदम सही |
अरे मैं तो कहता हूँ,
कि समय रहते नौजवान और
आनेवाली पीढ़ियाँ अगर खुले में प्रकृति से
रू-बरू होते रहे, तो शायद हम भी
गिद्धों के साथ साथ इनके किस्सों से भी
विलुप्त हो जाएंगे |



निवासी

Small Indian Kite
(*Milvus migrans govinda*)

©F. Sergio



प्रवासी

Black-eared Kite
(*Milvus migrans lineatus*)

©L. Narayan

Google us @

1. Density, laying date, breeding success and diet of Black Kites *Milvus migrans govinda* in the city of Delhi (India).
2. Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools
3. Raptors associated with airports and aircraft. In the book: *Raptors in human landscapes: adaptations to built and cultivated environments*: Page # 315-323.
4. <https://delhikiteswixsite.com/121212>





You all can help !
Ask us @ : delhikiteswii@gmail.com
Follow us on Twitter : @delhikites

Acknowledgements

- Director, Dean and Research Co-ordinator, WII
- Forest Dept. Delhi And U.P. : Delhi Zoo, Delhi Univ, Civic Bodies, Police and Citizens
- Black Kite Project Team , friends and well-wishers



©delhikites