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BLACK KITE PROJECT

PHASE-III

Final Report

Partners

Raptor Research & Conservation Foundation

Estación Biológica Doñana CSIC

Microwave Telemetry, Inc.

University of Oxford

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Behavioural Ecology of Black Kites *Milvus migrans* subsisting on urban resources in Delhi

(August 2016- July 2018)

Summary

The research team working in the National Capital territory, since December 2012, and through major funding support from the Raptor Research and Conservation Foundation (RRCF), envisioned a long collaborative term study around the urban adaptations of a large raptor, the Black Kite *Milvus migrans*. Supervised since its inception by Profs. Y. V. Jhala and Q. Qureshi from the Wildlife Institute of India, and Dr. F. Sergio of CSIC, Spain, this project is a unique attempt in the Sub-Continent to holistically unravel the adaptations around Black Kite's densest urban settlement in the world. We have now established how human cultural practices and attitudes may well be the most defining dimensions of the urban niche of synanthropes like Black Kites (Kumar et al. 2018). Thus, the third phase (August 2016 – July 2018), was a comprehensive assessment of the breeding ecology of Black kites, and their aggressive interaction with residents along the sampled urban gradient within the megacity of Delhi. For this, we used the habitat selection criteria of kites (Kumar et al. 2018) and inspected the behaviour of breeding kites at 101 territories (total 657 visitations), and tested their offspring defence (Kumar et al. *in review*). We found that defence increases with proximity to ritual-feeding sites and availability of offal, apart from progression in the breeding stage. This period also included the beginning of Phase -IV, an attempt to understand the migration of the *Milvus migrans lineatus*, the subspecies from the Central Asian Steppes wintering in the urban quarters of the Subcontinent from September to April every year. We deployed 13 GSM e-obs tags and 5 GSM tags from Microwave Telemetry Ltd. USA. These efforts were preceded by Phase-I of the project (December 2012 – June 2014) that focussed on basic natural history observations (Kumar et al. 2014), and the Phase-II (July 2014 – July 2016) which further extended the efforts to cover more sampling units, focusing on the aspects of habitat, behaviour and population ecology. The project has now entered its intensive-publication stage, as substantial data have now accumulated to enable high-level publications on international scientific outlets, with three publications lined up and ready to enter the genetic and disease components, apart from movement ecology. Finally, the project has incorporated through these initial years: (1) a remarkable amount of environmental education of Delhi citizens; (2) the Master thesis and near -completion of a PhD thesis by N. Kumar at an institute of repute (Oxford University, Department of Zoology, Edward Grey Institute of Ornithology); (3) completion of a Master program by U. Gupta at the Department of Geography of Oxford University; (4) training of more than 100 volunteers and some of them joining institutes of national and international reputation. All in all, the overall research team is extremely satisfied of all the progress and research formation attained and eager to move on to expand and intensify the project even more.

1. Background

Urbanization is one of the most radical environmental changes caused by human beings worldwide (Grimm *et al.* 2008 and Pauchard *et al.* 2006) and attention to its impacts on biota has been growing steadily over the recent decades (Seto *et al.* 2012 and Sodhi *et al.* 2004). It is known to be deleterious on most species but in certain adaptable species, it can have positive impacts. In urban areas, species sufficiently plastic in their response to changing environment can become commensal with humans, exploiting and benefitting from garbage, incurring profits from favorable microclimate and protection (Chace and Walsh 2006 and Marzluff *et al.* 2001). In most developing countries, poor focus over the repercussions of this rapid urban sprawl on the native flora and fauna has altered urban biological communities (Seto *et al.* 2012). There have been few intensive studies in urban environments, especially for mega-cities, for urban areas of tropical latitudes and for species at higher trophic levels (Chace and Walsh 2006). Top trophic species, like Black kites, are usually considered more specialized than lower trophic level species (Ferguson-Lees and Christie 2001 and Newton 1979).

The Black Kite is a medium-sized raptor, currently considered as one of the most numerous and successful birds of prey of the world (Ferguson-Lees and Christie 2001). It is an opportunistic feeder, capable of reaching extremely high densities where food concentrations allow it (e.g. review in Sergio *et al.* 2005 and Malhotra 2007). It may occupy habitats which range from fully natural to completely urban (Ortlieb 1998, Ferguson-Lees and Christie 2001). Such adaptability allows it to exploit human-modified habitats, affording it a generally favourable conservation status (e.g. Sergio *et al.* 2003). In India, the species is strongly associated with human settlements and acts as the main avian predator of the urban ecosystem (Kumar *et al.* 2014, Kumar *et al.* 2018). Previous research from the city of Delhi (Desai and Malhotra 1979, Galushin 1971, Kumar *et al.* 2014) showed that that these birds were stable in their overall breeding density since the 1960s. Kites, like most raptors, often exhibit exigent ecological requirements (Newton 1979). Though mainly recognized as city scavengers, presence of live and wild prey in their diet has been frequently reported (Ferguson-Lees and Christie 2001, Kumar *et al.* 2014 and Naoroji 2011). Within Delhi, kites nest in trees (i.e. they will need green space), or, less frequently, on anthropogenic structures, which amount to less than 10% of the overall nests. The nest substrate in the form of trees is readily available in the city. As the major predator in a city which affords them plenty of garbage-based food, these birds further enjoy a favourable attitude by local people to wildlife, which allows them to breed undisturbed in the immediate proximity of large human concentrations (Galushin 1971). Breeding in their dense colonies in the city of Delhi, these human commensal birds exhibit a moderate breeding success, where approximately 50% of the pairs successfully raise chicks to fledging (review in Kumar *et al.* 2014).

The resulting high density, often reached by this species in its southern Asian breeding quarters, offers a unique opportunity to replicate, extend and compare the reported individual-level and population-level patterns and processes reported for European populations (e.g. Bustamante and Hiraldo 1988, Hiraldo *et al.* 1990, Sergio 2003 and Sergio *et al.* 2004, 2011, 2014, Veiga and Hiraldo 1990 and Viñuela 1996, 1997a, b, 1999 and 2000). In particular, some of these studies, published in the 1990s, have been ground-breaking, with very detailed analyses of laying asynchrony, hatching asynchrony, sibling rivalry and brood reduction. They have become model studies for this sort of analysis, especially for raptor biologists (Hiraldo *et al.* 1990, Veiga and Hiraldo 1990, Viñuela and Bustamante 1992, Viñuela 1996, 1997a, b, 1999 and 2000). One of the main findings of the above studies was that food availability acts as a proximate factor that modulates brood reduction through sibling fights. This would fine-tune brood size on food availability when the latter is unpredictable, especially at the time of laying.

In the Delhi population, hatching asynchrony and brood reduction is common and Black Kites nest across steep gradients of urbanisation that impose substantial variation in food supply (Kumar 2013, M.Sc. thesis; Kumar *et al.* in prep). To study such links between brood reduction, food availability and urban landscape structure, we use camera-trapping devices (n= 18 from 2015 – 2018) positioned in nests, sampling all the urbanization gradients, and to integrate such data with regular visits at the same nests, so as to gather estimates of hatching asynchrony, brood reduction, chicks' growth rates, and the behaviour around nest defence and decoration. This will allow us to test: (1) how the components of urbanization (e.g. human waste-management, meat-tossing practices, human density, etc) translate into parental provisioning performance and diet composition, with repercussions on nestlings' growth, condition, stress levels and survival; and (2) how intra-siblings fights and killings may mediate such relations.

2. Research on Behavioural coexistence with humans by Black kites along a steep urban gradient: coping mechanisms and their consequences

Aims and Rationale

In this phase, we investigated how behavioural traits may exhibit the capability of kites to cope with an urban environment and exploit the opportunistic offers. An extension of this urban resource utility is in the form of artificial materials that this species is known to use to decorate its nests as a threat against conspecific territory intruders (Sergio et al. 2011). Thus, we focused on two behavioural traits that span a range of responses and consequences to close coexistence with humans: (1) fleeing distances from humans when perceived as a risk, (2) physical attacks on humans when these approach kites' nests,

Nest defence

Animals in urban habitats often exhibit bolder personality or tameness towards humans. Growing research suggests the possibility of regulation of this boldness either inherently (e.g. genetically), and/or because of individual-level variations in personality traits (and its plasticity) which may limit behavioural flexibility (Evans et al. 2010).

In Delhi, kites have been observed to be extremely aggressive towards humans when they approach their nests (and up to 250 m from it, Malhotra 1991, 2007, pers. obs.). This causes an intriguing situation where human beings, that are normally tolerant of wildlife within the city, could potentially become intolerant under certain situations, such as when kites' physical attacks target small children playing in parks or in a private house garden. Furthermore, breeding kites guard a small territory against conspecifics who attempt to either take over their territory or predate the nest contents (author's unpublished data). Such variation may enter the picture of the cost-benefits ratio of adaptation and exploitation by kites of an urban environment. To better understand such links and to elaborate solutions for potential conflict situations, we investigated the factors, which may predict elevated aggression by certain individuals and how such attack-frequency may change along the urbanization gradient under the following rationale. Thus, in light of a suggested correlation between behavioural boldness and adaptation to an urban environment, we have explored the associations in the level of aggressive nest defence by parent kites and the level of human settlement around their nest.

Fleeing distance

Many animals tend to flee when approached by humans (Blumstein 2006). According to Eason et al. (2006), flight initiation distance (hereafter FID), a commonly used estimate of this trait, is largely governed by a multitude of factors. They range from the history of human persecution, previous negative experiences with humans, distance to the nearest refuge, and type of approach (e.g. direct by a staring person), personality boldness, body

size, etc. Overall, most previous studies have supported the idea that FID could be a useful integrated measure that incorporates the overall balance of the above costs and benefits, as perceived by the animal. In the context of urban Black Kites in Delhi, where breeding and non-breeding birds could be expected to perceive human threats in different ways, human cultural practices .e.g. ritual meat tossing could further enter the picture of FID decisions (Clueas and Marzluff 2012). An individual kite may have to approach humans for food during such feeding episodes, or attack them when they approach its nest. Here, we examined how FID varies along a steep urbanization gradient and in relation to human density and prevalence of cultural practices such as meat tossing. In particular, we investigated whether individuals that occupy densely inhabited sectors of the city are more tolerant of proximity to humans (lower FIDs) than those that occupy more rural portions of the urbanization gradient. We hypothesised that kites are expected to exhibit potential segregation by personality, or micro-selection of bolder individuals through high natal philopatry and local recruitment (Evans et al. 2010).

Field procedures

For offspring nest defense analysis, we systematically surveyed kite nests during 2013–2016 at 24 plots of one km^2, which were randomly stratified within Delhi (1500 km^2) 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 101 nests and 657 defense trials, 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). 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 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).

We measured the FID as the distance from the observer to the bird when the latter first took flight, while the "starting distance" was the distance from where the observer started walking directly towards the bird (Møller 2010). This measurement was done on basis of field observations where the breeding birds allow a much closer proximity (the cost-benefit decision of guarding or abandoning the nest towards a possible human predator). To estimate such distances, we sampled 101 breeding territories, through 657 visits (2013-2016), along the whole urbanization gradient. The measurement was done using a laser rangefinder (model: Hawke 500). Having completed the data analysis, the manuscript on the FID of Black Kites in Delhi is under preparation.

Summary of the manuscript on Offspring Defense under publication consideration

Life history mechanisms that allow animal species to exploit urban resources, which entails specific behavioural adaptations to cope with rapidly expanding urban habitats, and frequent proximity to humans, has picked academic attention. A particular case of conflicting decision framework faced by animals in urban environments lies in the modulation of defence of their offspring against the potential danger represented by humans, an aspect that has received scarce research attention. We studied 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 subsist on a diet dominated by human waste and meat offered through philanthropic bird feeding practices. Likelihood of higher 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 spatially characteristic activities by humans in the city streets, their cultural practices of ritual feeding, and their waste-management, which promote higher human-animal familiarity. 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.

Fig 1. An experimental trial to test the aggressive nest defense by a breeding kite pair in the National Zoological Park. Here, a new volunteer is seen wearing the harness usually worn by the tree-climbing assistant who carries the equipment in similar fashion. This experiment aimed to test the ability of individual human identification, as reported by Malhotra (1991).

3. Summary of the research efforts (2016- 2018)

At the moment of writing, currently available sample size for camera trapping data curation, growth curves, and eco-physiology is:

n = data from 89 nestlings for which growth curves have been adequately curated. The data is being used for the subsequent manuscript in preparation, dealing with the demographic parameters of the long term monitoring data.

n = 350 fledglings (from ~ 200 nests), and 100 *Milvus migrans lineatus* for which feathers have been collected for corticosterone analysis.

n = 18. Data curation has been accomplished for 18 nests equipped with camera-trapping devices.

All the data on growth from previous field seasons are already available in Excel datasheet format. The data entry and analyses of camera-trapping images is currently being conducted and will be finished by August 2018. Information on the breeding ecology, behaviour and nest decoration will be obtained from the same.

Fig 2. A kite nest with a typical clutch of two eggs built on a *Eucalyptus* tree in the city. The nests are generally found lined with materials sourced from nearby areas (here: dung, green leaves, chicken feathers, newspaper, dry grass, etc).

Movement ecology (Phase IV): n (*lineatus*) = 19; n (*govinda*) = 3

Through 2014-2018, we have deployed over 20 Tags to monitor movement of Black Kites in the city, as well the migration routes. We aim to accomplish the sexing of the birds between August-November 2018 and communicate a paper on difference in movement and migration patterns based on the sex. Moreover, we have samples to test the genetic differences of the two subspecies. We have already been providing RRCF with the latest data on tracking of the bird wearing tag number 6244. With a screenshot of this bird displayed on the website, people can see in real time, how kites' journeys connect Delhi to such faraway places as the Mongolian steppes (through kites crossing barriers such as the Himalayas and the Chinese desert north of it). This is an ideal accomplishment both for research, for scientific dissemination and public education. We have encouraged several schools of Delhi adopt a tag, and appreciate nature, as an attempt to fulfil **Aichi Biodiversity Targets, CDB (https://www.cbd.int/sp/targets/).**

Fig 3. A typical roost of Black -eared Kite *Milvus migrans lineatus* in National Zoological Park, Delhi.

Current available sample size for growth dependent on sex and hatchorder

n = 89 (from 60 nests); With consultation from our supervisors, we shall collect more data if needed to test differences of male and female growth rates in different gradients of urbanization to understand the effects of sibling rivalry on growth and stress.

Current available data for ecophysiological and pathological studies"

n=300 blood smear slides from *lineatus* and *govinda* birds.

n= 180 blood plasma samples from *lineatus* and *govinda* birds.

n= 200 slides and samples from chicks

These would be analysed to see the parasite load and diversity.

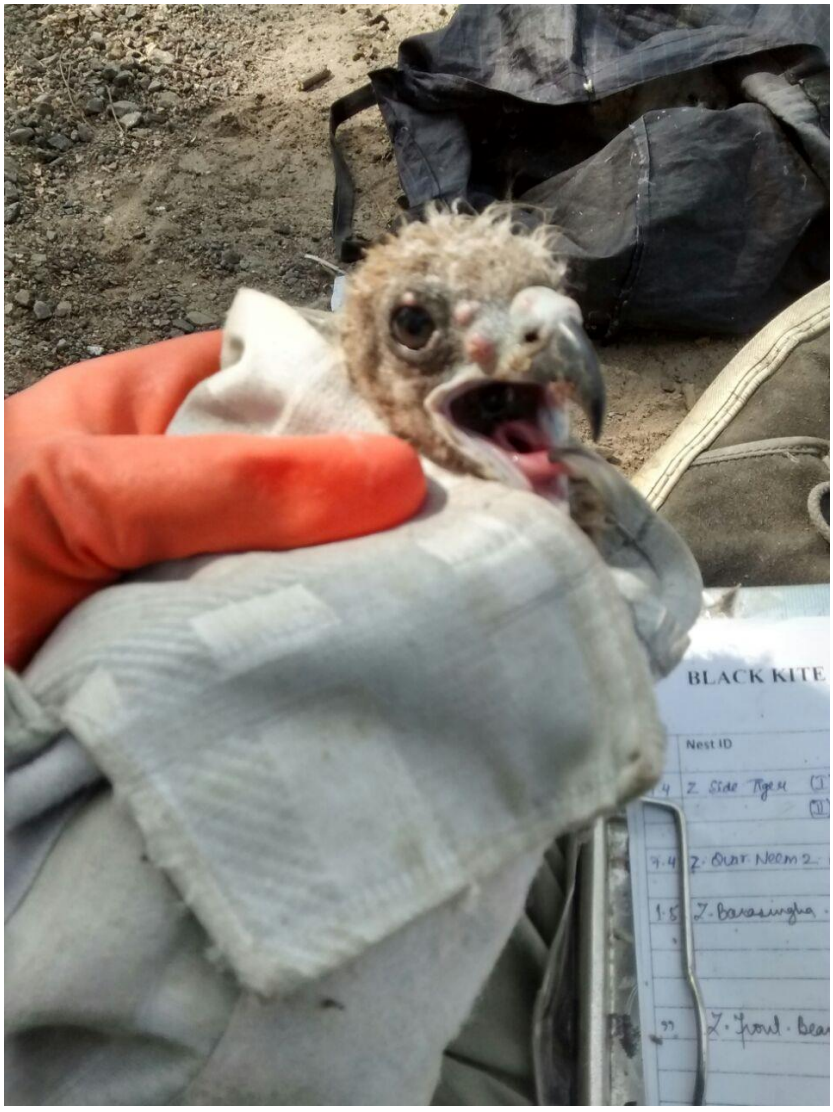

Fig 4. A kite chick affected with avian pox lesions.

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4. Movement Ecology (Radio telemetry) of Black Kites *Milvus migrans*

Delhi has proven to be the densest breeding ground for Black Kites *Milvus migrans govinda* and a wintering site for more than 10,000 Black eared kites, whose numbers reduce drastically with the onset of summers. Between April 2016 and April 2018, we were able to capture about 100 Black eared kites, and deploy 18 GPS-GSM tags (5 from Microwave and 13 from E-Obs) to monitor their migratory pathway. Using the per-minute GPS locations and accelerometer data, we aim to study their decisions during migrations, and the breeding grounds being used from this data. We were also able to tag a resident female kite, to monitor its movement during, and after the breeding season. The local kite helped build a better understanding of how kites opportunistically use the philanthropic meat offerings from the neighbouring Muslim colonies. Blood samples collected from the trapped individuals will be analysed for phylogenetic differences and to check the disease load.

Table 1. The current location of the birds with E-obs tags are depicted in the table, last updated on 17th August 2018.

Sl.	Tag #	Deployment	Last Data Relay	Location last updated
1	6242	27-03-2018	21-08-2018	Russia
2	6243	15-04-2018	21-08-2018	Kazakhstan
3	6244	13-03-2018	21-08-2018	Mongolia
4	6245	30-03-2018	21-08-2018	Mongolia
5	6246	21-03-2018	21-08-2018	China
6	6247	12-04-2018	27-04-2018	Haryana, India
7	6248	31-03-2018	03-07-2018	Russia
8	6251	07-04-2018	12-04-2018	Haryana, India
9	6252	08-04-2018	21-08-2018	Russia

10	6253	07-04-2018	21-08-2018	Russia
11	6256	09-03-2018	21-08-2018	Russia
12	6257	13-03-2018	21-08-2018	Russia
13	6259	30-03-2018	21-08-2018	Russia
14	865	29-04-2017	21-08-2018	Russia
15	866	26-04-2017	21-08-2018	Mongolia
16	867	28-04-2017	11-07-2018	Russia
17	868	29-04-2017	21-08-2018	Mongolia
18	869	22-04-2017	21-08-2018	Rajasthan, India

We believe that having deployed PTTs would immensely benefit the educational component of the study (see supporting information), because of the possibility to show the journeys to China, Mongolia, or Russia would likely leave many people, especially children, deeply fascinated. It would also give their teachers much to explain about the importance of conservation even in an urban setting. This is especially important in a historical era of skyrocketing urban sprawl, where 70% of the world population is expected to be concentrated in cities by 2050 (according to UN global projections), and even more so in developing and tropical countries. For large crowds, their urban coexistence with study species like ours will be their only possibility of a connection with nature.

Overall, the idea to show on a map and in real time, how kites' journeys connect Delhi to such faraway places as the Mongolian steppes, through kites crossing barriers such as the Himalayas and the Chinese desert north of it, would be an ideal accomplishment for research, for scientific dissemination and public education. We aim to make several schools of Delhi adopt each of the eighteen tags. We wish to nurture appreciation for nature in the new generation, fulfilling **Aichi Biodiversity Targets, CDB (https://www.cbd.int/sp/targets/).**

a) Background and Rationale

Birds exhibit the most spectacular and farthest displacements to accomplish daily and periodic movements while foraging, breeding and migrating (Newton 2010). 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 2013). Such impacts within rapidly evolving urban systems, and its associative changes around global human domination respond to changes in microclimatic factors and night-time light intensity (Anonymous 2016), spatio-temporal availability and predictability of habitable landscapes, foraging resource, and nest substrates (Kumar et al. 2018). Rapid restructuring of urban biological communities (e.g. sympatric competitors, facultative migrant scavengers), and stochastic shifts in the role of *anthropodependents* (see Hulme-Beaman 2016), from the neutral commensal state, is a major concern of rapidly populating cities in the global South. Compared to their rural counterparts, these long and short-term changes modify the behavioural profiles of the individuals interacting with urban ecosystems [r3] (Isaksson et al. 2018). Therefore, studies involving commensal birds as model offer opportunities to investigate the proximate drivers of evolutionarily crafted daily and periodic movement strategies.

It is worth mentioning that the extant and upcoming megacities (cities with >10 million inhabitants, United Nations 2014) in the tropical megabiodiverse regions, flank the erstwhile continuous natural scapes, subjecting animals to selection pressures from urban impacts. Ensued relegation of native vegetation to the city parks, thereby, alters by the expected reduction in urban biodiversity (Savard et al. 2000), often leading to a higher biomass represented by a few taxa. While research on urban ecology grows exponentially (e.g. Mayer 2010), major sites that have received attention belong to the developed world, where urban physical outlook has not changed much through the last century. 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 rapid urbanization is heavily concentrated in such areas (Grimm et al. 2008; Malakoff et al. 2016). Furthermore, few terrestrial studies have compared sub-specific distinctions over utilization of urban resources, reflecting the saga of human-animal relationship, which has evolved through slow ebbs of socio-ecological changes in human habitation. Limitations in urban research rigour due to inadequate ecology-based framework also demands focus on the specific exploitations of humans by commensals, and how it impacts the socio-cultural expressions of citizens to commensals.

To contribute to these overlooked areas, we examined the impacts of urban resources on the spatial ecology of Black Kite *Milvus migrans,* a synanthropic facultative avian predator in the tropical megacity of Delhi, India. Here, we demonstrate that the urban movement choices by the two sub-species found in the sub-continent are dependent on remnant habitat patches, and are tightly intertwined with human activities

and religio-cultural practices (see Kumar et al. 2014, 2018). It includes predictability of enormous food resource like ephemeral dumping and sanitary landfill sites, which greatly influence the spatial distribution of food subsidies and commensal behaviour.

The Black kite *Milvus migrans* is a medium-sized raptor, considered the most successful facultative avian predator. However, intensive studies on this species have focused disproportionately on a few European populations (e.g. Viñuela 2000; Blanco *et al.* 2003, 2007; Sergio *et al.* 2011a, b), while relatively little is known about the sub-species and populations of other continents (Ferguson-Lees & Christie 2001). Throughout its distribution, they are known to perform North to South migration, with resident breeding sub-species found in tropical and sub-tropical systems nearer to the equator. Detailed knowledge of their migration routes or of their distribution during the non-breeding season, are often completely unknown or only suspected (Naoroji 2006). Human dominated urban systems of the Indian sub-continent harbours hundreds and thousands of kites, arguably the densest population of kites in the world, due to its capability to withstand anthropogenic habitat change and even breed amidst dense populations within cities (Ferguson-Lees & Christie 2001)

Individuals of *lineatus* sub-species migrate south from their breeding grounds in central-northern Asia while the native, resident subspecies *M. m. govinda* is synurbic or *anthropodependent* (Francis & Chadwick 2012), i.e. it occurs almost exclusively in close association, exhibiting relatively higher breeding densities with humans in towns and cities (Naoroji 2006). While large concentrations of *lineatus* individuals have been noted at several sanitary landfills in the Indian cities, it is unknown whether each individual spends its full non breeding period at a single dump, within a single town, or whether they move between towns, or even nomadically over enormous areas as accomplished by European Black Kites in Africa (Sergio et al. 2014). In Delhi, where this study was conducted, kites breed throughout the city, often a few meters from human habitation, reaching extremely high local densities, afforded through the exploitation of human food subsidies facilitated by inefficient refuse disposal and by religious kite-feeding practices (see details in Kumar et al. 2014; 2018). There is a huge lacuna over the niche segregation between the resident and the migrant sub-species. The fact that two morphologically very similar taxa can live side by side within the same landscape poses interesting questions about the mechanisms that may mediate their coexistence (e.g. niche separation).

Field procedures

Throughout our sampling regime, trapping was accomplished near the sanitary landfill of Ghazipur (n= 19), National Zoological Park (n=2), and Delhi University North Campus (n=1), within the city of Delhi. Birds were trapped using mist nets and/or an improvised *Bal-chhatri* baited with carrion. The *lineatus* were identified by their broader white carpal patch on their underwing, black plumage in the lateral-rear of the eyes, bluish-white cere and tarsus, more thickly feathered tarsi, larger size and sturdier and appearance than *govinda*

birds (see DeCandido *et al.* 2013, Forsman 2003 & Naoroji 2007). We deployed the platform transmitter terminals (PTTs) using tubular teflon harness, the one used on Black kites in Doñana National Park (Spain). This method has been shown not to impact kite individual health and fitness through a comprehensive assessment (Sergio *et al.* 2015). All kites trapped for satellite and GPS marking were accurately weighed and measured. We also collected samples of blood and feathers to sex all birds by using molecular methods, and to obtain various physiological estimates of nutritional condition.

Black-eared kites were equipped with the GPS satellite tags of the model 25 gram Solar GSM PTT (n=5) manufactured by Microwave Telemetry Ltd; and 25 gram GSM-GPRS PTT manufactured by e-obs GMBH, Germany (n= 13). The *govinda* individuals were tagged with a 22 gram Solar Argos/GPS PTT (n=1), and with an e-obs 28 gram Solar GPS PTT (n=2). The PTTs represented < 4 percentage of the birds' body mass. All the tag-models recorded GPS positions and the heading, elevation and speed of the bird under different configurations throughout the year. The GSM tags were actually configured to relay data at shorter intervals of every 1-2 minutes, to obtain more refined estimates of movement strategies over the fine-grained urban landscape (e.g. fine-grained exploitation of urban canyons for flying, or of meat-tossing points, easily lost by hourly fixes.

By marking several Black-eared kite individuals with GPS or GSM-satellite tags and *govinda* kites (n=3) with GPS tags, we: (a) defined the migration routes and performance of the *lineatus* subspecies; (b) determined their breeding areas and migratory connectivity; and outlined how the two sub-species differentially use the Delhi urban environment during September – May each year. Tracking data were obtained either from the hand held download for the GPS e-obs PTTs, or from the Microwave Telemetry Inc. and Movebank online repositories.

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Supporting Information

Fig 5. The research team gets hands-on training on affixing a platform terminal transmitter (PTT) to a kite from Dr. Fabrizio Sergio, and Prof. Y. V. Jhala (in the background).

Fig 6. The end-knots of the teflon harness are secured carefully by a cable tie, and a few drops of superglue. These GSM tags are expected to comfortably transmit data for 2 -3 years.

Fig 7. Black Kite project team with the kite wearing the GSM PTT # 6244. The live route of this bird can be traced here: http://www.raptors.net.in/projects/

Fig. 8. Black Kite Project Research team affixing a GSM tag to a Black -eared Kite (*Milvus migrans lineatus*). The tag in the image has a solar panel on the top, and is affixed on the birds using a tubular teflon harness.

Fig 9. The tagged bird is given a final check before its release. This dorsal image repository also helps in maintaining the database for age estimation based on plumage and other morphological features.

Fig 10. The kite pictured above, wearing a PTT, is ready to be released. Here, the bird is allowed to flap its wings few times before its first flight with a GSM tag on its back.

Fig 11. Kite wearing tag # 6244 is successfully released by the field assistant Laxmi Narayan.

Fig 12: Migration of Black Eared Kites which are now moving in their breeding grounds in Russia and Mongolia (tracks of 5 Microwave GSM tagged birds)

Fig 13. Migration of Black-eared Kite No. 6244 which is now moving in its breeding grounds in Russia and Mongolia.

Fig 14. The research team in the above image has set up a two-way communication with a GPS tag affixed on a kite of the resident subspecies *Milvus migrans govinda*. The telemetry data form the transmitter can be read using a hand-held, portable base station. The same base station is used to re-configure the tag using a laptop and an omni antenna fitted on the roof of the vehicle.

5. Achievements: 2016 - 2018 (Phase - III)

We have successfully trained >100 university students on basic field research, out of which 25 have joined institutions of national and international repute for their higher studies (Oxford, Imperial, Ireland, India: WII, JNCASR, TERI, DU, FRI etc). Alongside, with the team of volunteers, we have also imparted conservation education to ~ 45,000 Delhi citizens, as a mobile conservation education unit through the years of field research. Additionally, we have voluntarily lectured in 5 schools and 3 colleges, and ran a workshop led by Ms. Urvi Gupta, for **Department of Science & Technology, Govt. Of India's** initiative INSPIRE. In March 2018, Urvi won the **best talk award** for our work on Black Kites, at the **Society for Conservation Biology** conference, held at Amity University, Noida.

(i) Peer reviewed publications: (Published and in review)

Kumar N, Jhala YV, Qureshi Q, Gosler A. and Sergio F (Submitted) Uncomfortable but revered neighbours: human-attacks by an urban raptor are tied to human subsidies and religious practices. *Scientific Reports*

Kumar N, Qureshi Q, Jhala YV, Gosler A. and Sergio F (*2018*) Offspring defense by an urban raptor responds to human subsidies and ritual animal - feeding practices. *PLOS One* (*Decision in Process post first revision*)

Kumar N, Gupta U, Jhala Y V, Qureshi Q, Gosler A. 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 ecosystems*, 21(2), 339-349

Kumar N, Dhananjai Mohan, Yadvendradev V. Jhala, Qamar Qureshi & Fabrizio Sergio (2014): Density, laying date, breeding success and diet of Black Kites *Milvus migrans govinda* in the city of Delhi (India), *Bird Study*, 61 (1), page 1-8

(ii) Featured mentions and Publications for Science Communication (Published and invited)

Kumar N, Gupta U, Narayan L. (invited for 2018-19) **How black kites decide where to build a nest,** *Frontiers for Young Minds* (a journal for 8-15 year olds)

Gupta U, Singh H. (2017) **Of Flying Tigers**, *Imprint (Department of Zoology, St. Xaviers College, Mumbai)*

Thampi P. (2016) **Delhi's Kite Runner: An amateur curiosity that explains the effects of**

unplanned urbanization. *Economic Times.* Available at: https://economictimes.indiatimes.com/magazines/panache/delhis-kite-runner-an-amateur-curiosity-that-explains-effects-of-unplanned-urbanisation/articleshow/53889100.cms

Nair A. (2016) **The Last Flight**. *Sanctuary Asia*, 36 (8) Available at http://www.sanctuaryasia.com/magazines/features/10377-the-last-flight.html

(iii) Conference Proceedings (2016-18):

Gupta U, Kumar N, Jhala, Y.V., Qureshi Q, Barua M. and Sergio, F. (to be presented in October 2018) **Life in cities: human-animal interface, perceptions, and co-existence** *Student Conference in Conservation Science, New York, USA*

Gupta U, **Kumar N**, Jhala Y.V., Sergio F. and Qureshi Q. (to be presented in September 2018) **Human dimensions of urban niche of Black Kites *Milvus migrans* in Delhi, India.** *Annual Research Seminar, Wildlife Institute of India.*

Kumar N, **Gupta U**, Qureshi Q, Sergio F. and Jhala Y.V. (to be presented in September 2018) **Filth, cultural attitudes and urban architecture shape the breeding ecology of urban raptors** *Annual Research Seminar, Wildlife Institute of India.*

Gupta U, Kumar N, Jhala, Y.V., Qureshi, Q and Sergio, F. (2018) **Living in the city.** *Society for Conservation Biology- India Chapter, Amity University Noida*

Malhotra H, Kumar N, Jhala, Y.V., Qureshi, Q and Sergio, F. (2018) **Appreciating the urban commons; Successful synurbization of *Milvus migrans.*** *Society for Conservation Biology- India Chapter, Amity University Noida*

Kumar N, (2017). **Black kites in Delhi: A bird's eye view.** Urban Animals- New Delhi Workshop, by Wellcome Trust (organized at India International Centre)

Kumar N, (2017). **Delhi, the Kite Capital!** Human-Black Kite *Milvus migrans* co-existence in a rapidly urbanizing megacity. New Networks for Nature, Stamford, United Kingdom.

Kumar N. (2017) **Densest breeding raptor population in a megacity! Urban Ecosystem health and Black Kites in Delhi. Wellcome Trust- DBT, India Alliance meet at**

George Institute of Global Health (organised at Somerville College, University of Oxford)

Kumar N, (2016) **"Passive" Nature in anthropologically-architectured environments,** India Policy Day, University of Oxford, UK.

Gupta U, Kumar N, Jhala, Y.V., Qureshi, Q and Sergio, F. (2016) **Being a large raptor in a rapidly changing megacity of Delhi** *Student Conference on Conservation Science. Bangalore*

(iv) Grants (2016-18):

Grant: Alice Horsman Scholarship
Funding Agency: Somerville College, University of Oxford
Awarded to: Urvi Gupta
Grant value: £ 1300
Purpose: To deliver an oral presentation at SCCS New York, USA, in October 2018

Grant: Christina Howey Rising Scholar
Funding Agency: Microwave Telemetry Inc.
Main Investigator: Nishant Kumar
Grant Value: Charges for data acquisition from 5 GSM PTTs.
Grant duration: Oct 2018- Nov 2020;
Purpose: Migration of Black-eared kites *Milvus migrans lineatus* through the Asian migration flyway to Delhi: Implications for the conservation of Central Asian migrant birds and local environmental education
Weblink:http://www.microwavetelemetry.com/uploads/newsletters/2016_Winter/MTINewsletter_2016_Winter_page8.pdf

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

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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

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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 km^2 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 km^2. These were plotted randomly within Delhi (1500 km^2) so as to cover all its possible urban settings, from semi-natural to extremely built-up sites (details in 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,

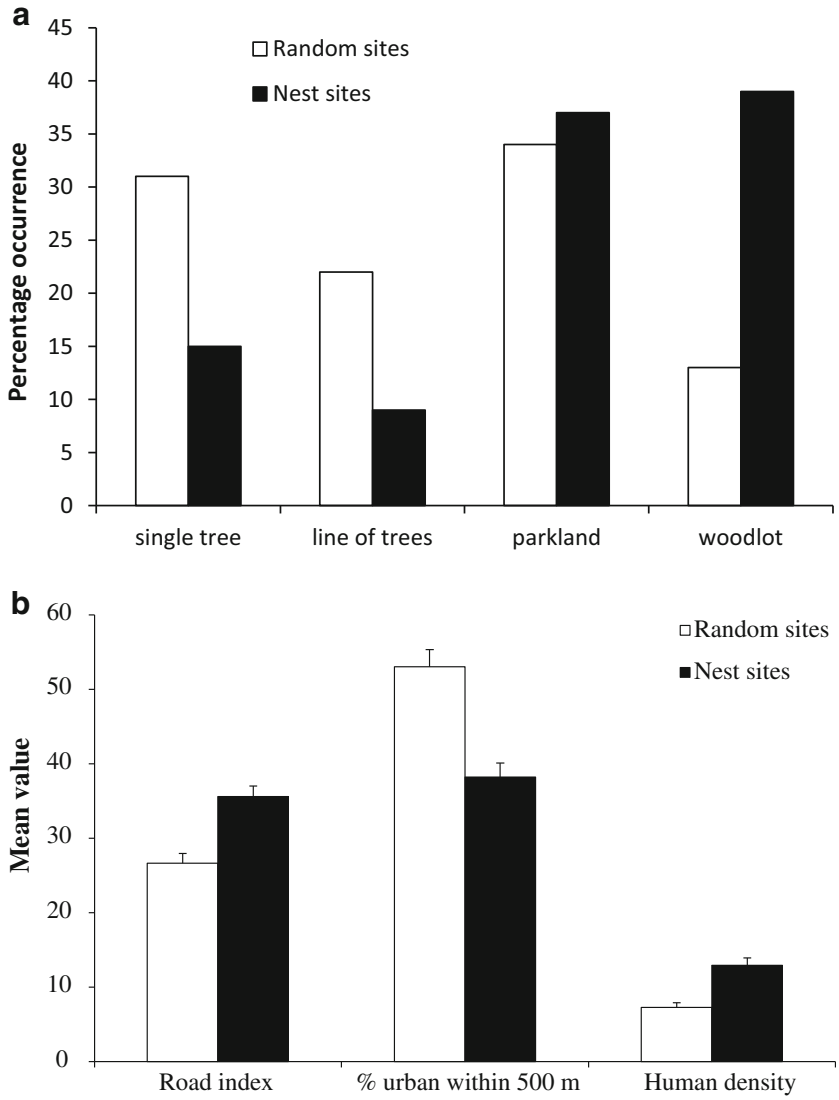

Fig. 1 Tree arrangement (Panel **a**), and index of road density, percentage urban land cover within a 500 m radius, and human density (panel **b**) at 100 Black Kite nests (black bars) and 100 random locations (white bars) in Delhi (India)

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 templet.

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

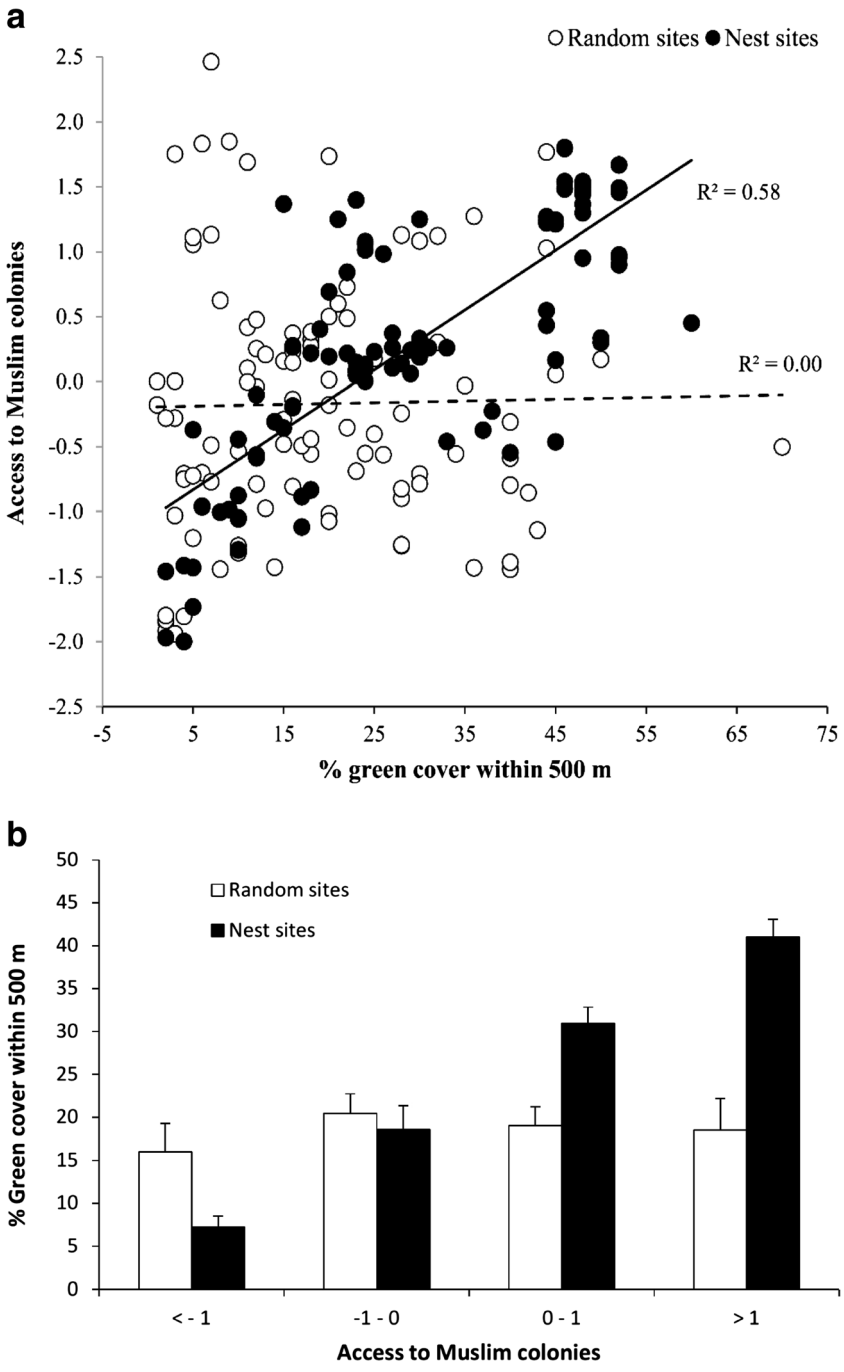

Fig. 2 Urban kites in Delhi selected sites for which access to Muslim colonies and vegetation cover positively covaried (panel **a**). Thus, they over-selected areas with abundant vegetation close to dense Muslim colonies, but avoided them when far from Muslim colonies (panel **b**). Access to Muslim 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

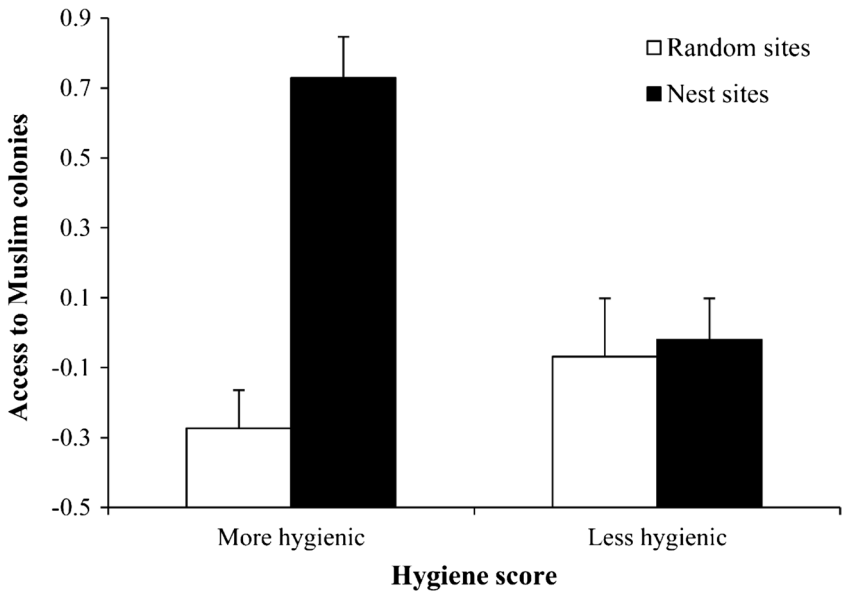

Fig. 3 Access to dense Muslim colonies was higher at Black Kite nests (black bars) than at random locations (white bars) when local hygiene levels were high, while inefficient refuse disposal (i.e. low local hygiene) "released" kites from dependency on Muslim ritual subsidies. Error bars represent 1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

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Online Resource 1

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

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

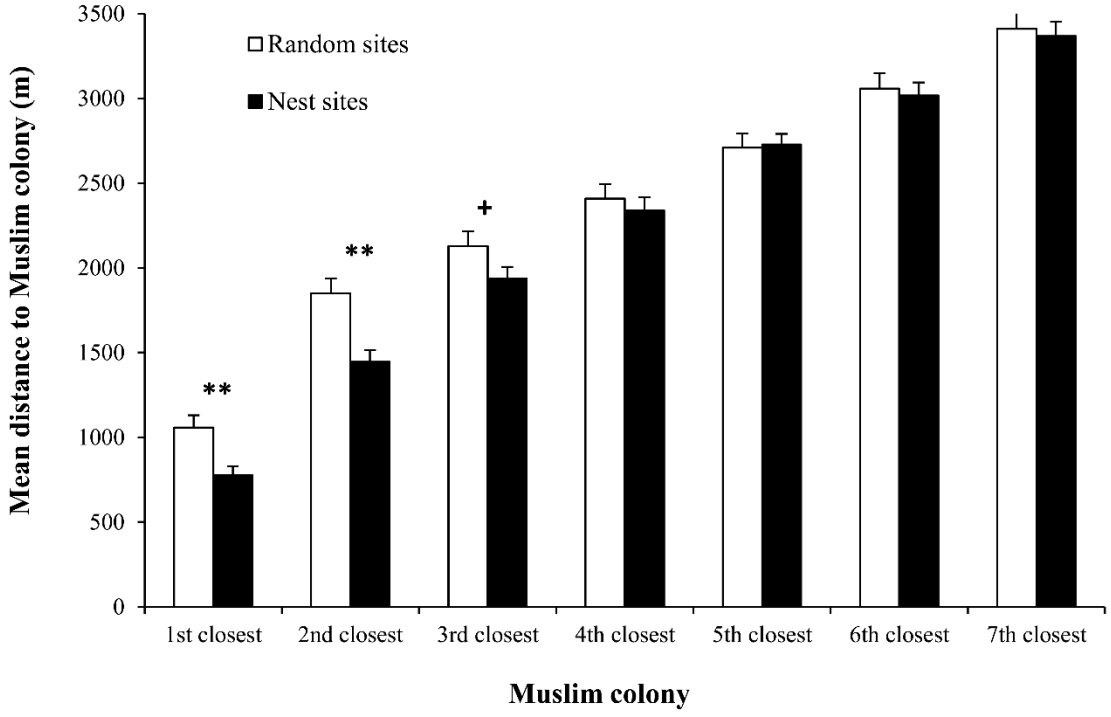
Access to human subsidies by Delhi kites: rationale and estimation

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 lebbeck* (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).