



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 km² and in constant, rapid expansion (Census organization of India 2011). It is polycentric and heterogeneous, with a multitude of urban

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

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

Field procedures

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

Breeding site characteristics

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

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

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

Statistical analyses

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

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

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

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

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

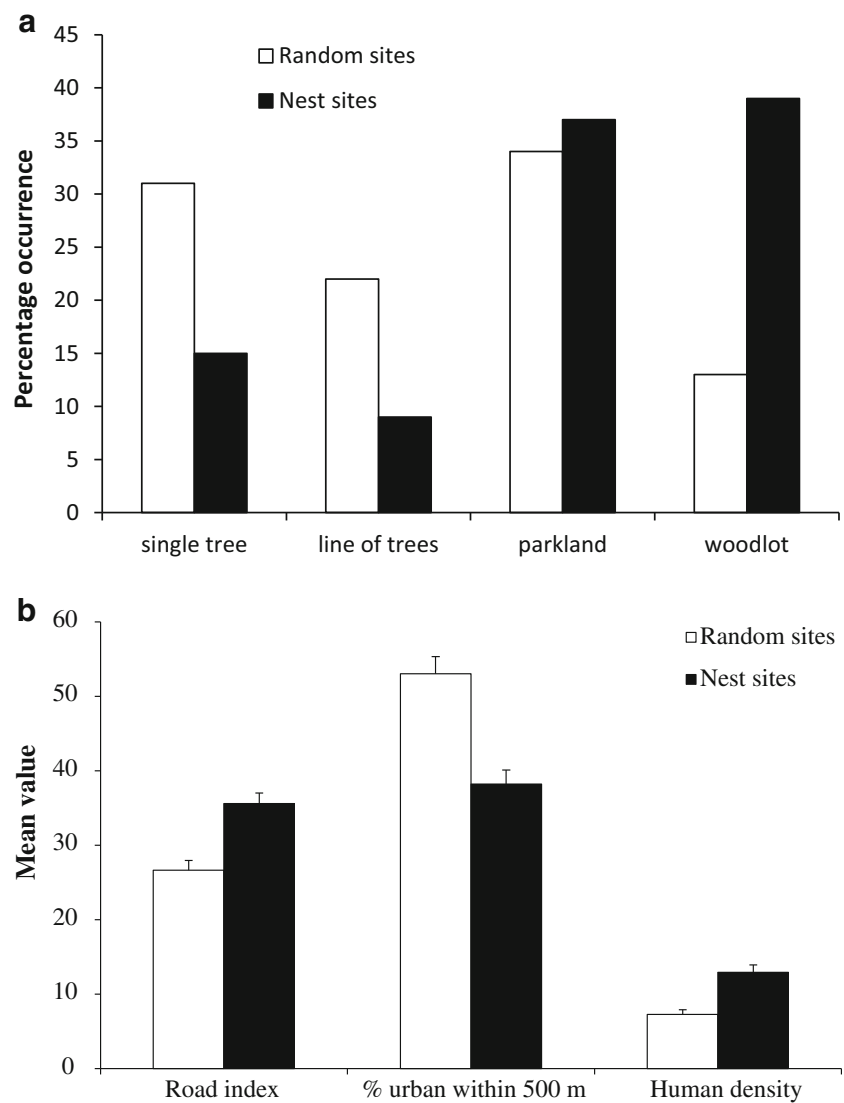
to the habitat selection logistic model on both the number of years that a territory was occupied and on the cumulative number of fledglings that it produced between 2013 and 2016. We predict that territories that were more frequently occupied were of higher quality and thus were more attractive to kites,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

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

Results

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

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



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

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

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

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

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

Discussion

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

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

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

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

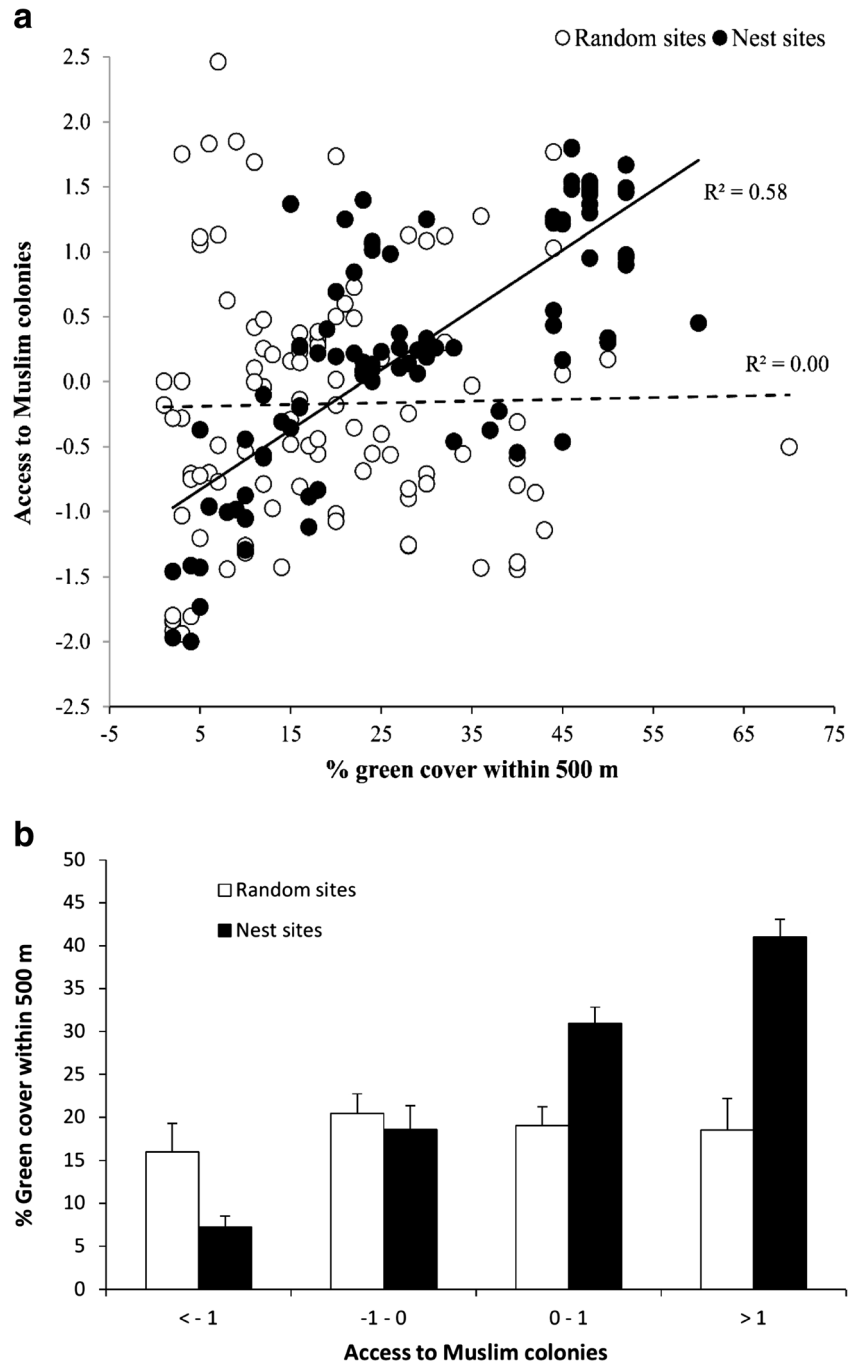
Second, while kites avoided high rates of built-up land cover, they simultaneously selected areas with high road and human density. Because human density was assessed in the streets, it equated to an index of human traffic and street-activity, and because refuse is often disposed of by people in a disorganized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

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

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

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

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



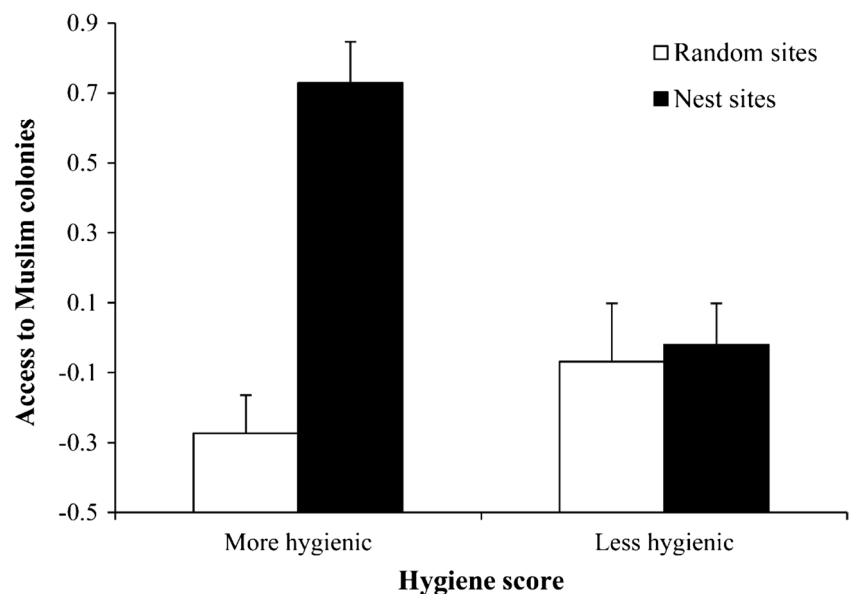
Templeton 2002; Danchin et al. 2004). The advantages described above were confirmed by the higher occupation rate and breeding output of territories in proximity to multiple Muslim colonies, which suggested that these sites were attractive to kites, that they contributed a disproportionate number of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

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

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

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

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



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

Conservation implications

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

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

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

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

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