Vulture loss and urbanisation correlations form blind spots for conservation and development

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Research Article

Keywords: Nature-based-solutions, urbanisation, wildlife restoration, Global South, scavengers, Ethnoecology, anthropomorphism, biocultural, biophilia, Social-ecological Systems

Posted Date: October 5th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-505472/v2>

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Abstract

Correlations in the timings of vulture collapse and rapid urbanisation in South Asia have affected the benefit trade-offs concerning conservation-breeding for vulture restoration. We show how the loss of vultures 30 years ago has led to the *extinction of experience* amongst people in South Asia who are co-adapted to various animal species within shared landscapes. We conducted ethnography, involving avian scavengers (vultures, kites and crows) in Delhi, to unpack how salience and charisma for avian scavenger's link with socio-cultural legends. Perceptions about avian scavengers were based on birds' appearance, behaviour, and ecosystem services. Anthropomorphisation mediated human-animal co-adaptation and drove ritual feeding of commensals that opportunistically consume garbage. Conflated with ethnoecology, such human-constructed niches supported enormous animal populations in the region and drove mutual tolerance. Prior evaluations of scavengers' niche from biophysical perspectives alone have, therefore, overlooked prior links between vultures and animal husbandry practices. It undermined competitive release on commensals that have responded by an increase in numbers and distribution, by taking advantage of ritual feeding and people's affiliative attitudes. The absence of vultures limits the availability of spaces where animal husbandry can be practised. Conversely, expanding built-up spaces, overhead wires, fake news, and interference from competing scavengers will be impediments to vulture restoration. Conservation policies should examine immediate and long-term objectives of solid waste disposal, considering the odds against the attainment of former functional ecology by vultures. We conclude that wildlife restoration in urbanising tropical landscapes is a moving target, necessitating policies sensitive to progressive loss and/or changes in associative heritage due to shifting economic and cultural practices.

Introduction

The decline in vulture populations and rapid urbanisation are temporally correlated events for vast human-use landscapes of South Asia and Africa (Botha et al. 2017; United Nations Department of Economic and Social Affairs- Population Division 2019). These correlations attribute in opportunistic proliferation of certain facultative animal scavengers, e.g., kites, crows, rats and dogs (Narayanan 2017; Onen and Bassey 2017; Williams, Balmford, and Wilcove 2020). Conversely, in built-environments, urban planning and local cultures affects animal ecology tied with socio-economically and culturally valuable ecosystem-services, e.g., García-Jiménez et al. (2021). Biodiversity conservation in urbanising landscapes, therefore, requires *transdisciplinary* research (Nagendra et al. 2014; Williams, Balmford, and Wilcove 2020) on several factors that may preclude success of traditional approaches (Plaza and Lambertucci 2020).

In case of avian-scavengers, the first of these factors is associated with the change in quantity, quality and spatial outlay of solid waste. Poorly disposed waste is a characteristic aspect of tropical urban ecosystems that support an extraordinarily high density of scavengers like vultures, kites, crows, dogs,

rodents, etc. (Galushin 1971; S. Kumar et al. 2017; Markandya et al. 2008; Newton 1979). Second, major socio-economic transitions in the region have been associated with several agricultural movements, e.g., the 'Green' and 'White' revolutions, and the development of milk cooperatives (Basu and Scholten 2012) in the late 20th century. Agricultural movements implied regional changes in capacity to raise livestock, affording resident and migratory avian taxa with opportunistic forage in the form of dead carcasses left in open fallow areas in urban villages like *Wazirpur* in Delhi. Scavenging-services, primarily undertaken by vultures, not only supported urban health and hygiene but also mediated the feasibility of raising livestock in tropical-cities, based on a network of carcass dumping sites in association with dairy-establishments. The spatial correlations between poor immigrant-settlements and abundance of opportunistic avian-scavengers are an outcome of traditional and/or informal livestock rearing in backyards (Sharan 2014). Third, raptor populations are typically limited by food and nest-sites (Newton 1979). In many tropical cities, relics of native vegetation, tree plantations and other man-made physical structures like towers and pylons have been studied to mediate accessibility of carcasses and human-offal for breeding and communally roosting avian-scavengers (N. Kumar, Gupta, et al. 2018). The final but perhaps most defining factor is the prevalence of cultural beliefs that sustain positive-attitudes and tolerance for vultures and other commensals and scavengers. Tolerance persists in South-Asia despite social legends which classify them as agents of death associated with bad omens, an aspect which currently impacts vultures in Africa (Botha et al. 2017; Buij et al. 2016; Dave 2005).

The traditional good-will of Indians to living beings (Galushin 1971) is a co-adaptation of how rural-areas, customs and socio-economic practices are still integrated across scales into local, regional and national-development (O'Bryan et al. 2018; Sietchiping et al. 2014). For instance, in addition to vultures' biophysical niche as obligate scavengers, their ecosystem services factored in sustaining socio-economic and cultural processes (Botha et al. 2017; MOEFCC 2020). Over many centuries, their gregarious feeding has been harnessed as a nature-based solution (O'Bryan et al. 2018) for the disposal of cattle carcasses. It supported bovine leather processing livelihoods (Van Dooren 2010; Sietchiping et al. 2014; Sinha 1986). 'Leatherwork' and 'leatherworkers' were segregated from main establishments near the carcass-dumping grounds (Sinha 1986). Alongside, vultures' scavenging also contributed to small scale industries based on the bovine bone remains- e.g., bone meal fertiliser units in proximity to carcass dumping sites (Van Dooren 2010; MOEFCC 2020). Studies have also reported vulture-human mutualism in Africa, e.g., see (Gangoso et al. 2013; Moleon et al. 2014). Further, *Parsi* (Zoroastrians) community practice *dokhmenishini* (sky burial) to honour their dead, by offering the bodies to vultures in *dakhma* (the *Tower of Silence*). This traditional funeral has been severely affected by the loss of vultures, forcing *Parsis* to choose from relatively less-sustainable methods like cremation (Van Dooren 2010; Iaccarino 2003).

In South Asian cities, importance of human-animal co-adaptation and socio-cultural factors are widely overlooked in very limited urban ecological studies (N. Kumar, Gupta, et al. 2019; N. Kumar, Singh, and Harriss-White 2019). Except for a coarse estimation for the overall Delhi's breeding raptor population, quantitative data for vultures and other raptors in this biogeographic region are extremely scarce (Galushin 1971; N. Kumar et al. 2014; N. Kumar, Gupta, et al. 2018; N. Kumar, Jhala, et al. 2019; Mahabal

and Bastawade 1985). Galushin estimated that vultures constituted 5% of ~3000 breeding pairs of raptors sampled in 150 km². Black Kites *Milvus migrans* were the most commonly breeding raptors (83% or 2400 of all breeding pairs), in a period before the regional vulture-collapse. Like other long living top-trophic organisms, large-sized raptors do not breed for the initial 3-5 years of their life (Newton 1979). The absence of information on the non-breeding populations of pre-adults and post-prime adults precludes holistic assessment of ecological dynamics. Understanding the ecology of non-breeding populations, therefore, requires higher attention in the case of opportunistic commensals, considering that superabundance of food can impact breeding success and survivorship that can locally substructure numeric responses to food-subsidies (Newton 1979). Finally, soaring avian scavengers like vultures and kites can fly anywhere between 30-125 km on foraging trips that require relatively larger sampling region for assessment of ecology and behaviour (Monsarrat et al. 2013). Their keen eyesight, social-learning and ability to navigate built-environment for foraging feature in various folktales, discussed below in detail (Potier et al. 2020).

Unlike the reintroduction of partial migrant Eurasian griffon (*Gyps fulvus*) in Europe (Kmetova–Biro et al. 2021), in the Indian subcontinent, rewilding captive-bred resident breeding vultures within or near the human use landscapes would face novel challenges accompanying urbanisation (Hayward et al. 2019; Seddon, Armstrong, and Maloney 2007). In the recent past, synurbic vulture populations were co-adapted to built-environment and people. However, in this decade, an estimated 65% or more of people in the Indian subcontinent that are below the age of 35 years have never witnessed the scavenging ecosystem-services of vultures (Census Organization of India 2011; United Nations Department of Economic and Social Affairs- Population Division 2019). Demographic and behavioural changes in human and wildlife populations lead to an *extinction of experience*. As a result, there is a loss of awareness of the birds' phenotypic and ecological salience (Hunn 1999). Considering highly interspersed peri-urban, protected and human-use landscapes within the developing regions of the world, scavengers' associations with food-subsidies are likely to increase proximity and exposure of wildlife to humans, and vice versa (Schell et al. 2021; Soulsbury and White 2016). Co-adaptations of people to various animal species within shared landscapes are, therefore, under major upheavals in rapidly urbanising ecosystems. Major gaps exist over understanding how people's perceptions modulate non-human animals' access to anthropogenic resources and shape human-wildlife interactions and mutual tolerance in South Asia (Alberti 2008; Anonymous 2016; Bergsten, Galafassi, and Bodin 2014; Folke et al. 2005; Hunn 1999; Levin et al. 2013; Lorimer 2007; Ostrom 2009; Rademacher, Cadenasso, and Pickett 2019; Soga and Gaston 2020; Soulsbury and White 2016).

While rare and endangered species get research and conservation attention, common species that provide valuable ecosystem services can aid public will for conservation due to relatively higher human-animal encounters (Gaston 2010). Despite the obvious significance of backyard species for humans in the urban environment, only few researchers have explored how information on changing perceptions for wildlife in the backyard may yield important insights into mechanisms of resilience enabling close coexistence with humans (Dunn et al. 2006; Marris 2013; Miller and Hobbs 2002). To contribute to these

overlooked aspects that concern wildlife restoration effort within or near human-use landscapes, we focused on common urban scavenging birds that are readily encountered interacting with residents in Delhi- Black Kites *Milvus migrans*, crows *Corvus splendens*, and vultures (*Gyps* spp. and *Neophron* spp.). We examined the 'affective attitudes' people have for these three taxa in South Asia, which is usually driven by co-adaptations that involve anthropomorphic beliefs. We conducted semi-structured ethnographic surveys on capturing complex mutual relationships between multiple human and nonhuman agencies, involving biotic, physical and socio-cultural factors that affect the benefit trade-offs with anthropomorphising commensals.

Methods

This study is part of a long-term research project (N. Kumar, Gupta, et al. 2019) on the ecology and ethnozoology of urban scavengers in Delhi. The city has rich birdlife and the world's second-largest urban human population of 29 million inhabitants (United Nations Population Division 2018). Ongoing urbanisation makes it a melting pot of cultures composed of people from across the Indian subcontinent (Bhagat and Mohanty 2009) (details in Supplementary material 1). We seeded this research to examine the ecological and biocultural impacts of regional vulture loss.

For this study, we adapted a Delphi-like ethnographic approach for the horizon scan of ethnoecological aspects associated with city's solid waste management to understand how a wide range of stakeholders and their interactions with avian scavengers characterised a tropical megacity's human-animal interface (Esmail et al. 2020; Mukherjee et al. 2015) (Fig. 1). Our field sampling has involved regular surveys since 2012 in Delhi at 32 randomly distributed plots of approximately 1 km². The design systematically covers all urban settings, from semi-natural to extremely built-up sites, including all the three sanitary-landfills (for details, see (N. Kumar, Gupta, et al. 2019; N. Kumar, Singh, and Harriss-White 2019); Supplementary material 1).

Ethnography followed a stepwise procedure. (**Stage 1**) We interacted with 27.03 (SE: 2.31) new onlookers within our sampling units during every field visit (see Supplementary material 1). Horizon-scans involved people who voluntarily engaged in conversations. They solicited direct inputs corresponding prominence of urban scavengers in the wake of vultures' local extinction. The overall sample for this voluntary availability of citizens who contributed to semi-structured horizon scan was 54060 (SE: 4620) (~250 field visits, every year, 2012-2021). We used iterated surveys, facilitated discussions, structured elicitation, and aggregation of individual perceptions and associations with animals to incorporate the full range of socio-cultural perspectives regarding opportunistic scavengers in the city. Through iterated interactions with new, random sets of respondents from the same stakeholder unit, we identified and mitigated typical individual-level psychological biases (Esmail et al. 2020). Our respondents revered or vilified myriad types of non-human animals, which contextualised their professional and/or socio-cultural conduct towards urban animals. Out of the total respondents, 826 contributors (designated as decision makers with respect to human-animal interface) were affiliated with stakeholder groups likely to have higher encounters with avian scavengers on a regular basis. Out of these decision makers, 5.7 % were affiliated

with academia and 5.5 % with NGOs (e.g., *World Wide Fund for Nature*, *Wildlife Trust of India*, etc.); 2.4 % were ritual feed-sellers (grains, fruits and meat-chunks); 9.3 % worked for the government (zoo, municipality, health workers) and 2.1 % for religious organizations (priests/clerics). About 75 % of overall subjects were associated with the informal waste-work (butchers, chicken and fish market cleaners, rag pickers, municipality contract labourer, contractors). Taking the timeline of local extinction of vultures into account, we classified the respondents in two categories, based on the age classes of more or less than 35 years.

In **Stage 2**, before every iteration step, the lists of responses were thematically organized to identify the correlations in respondents' socio-cultural and professional backgrounds. Here, we also scanned the immediate surroundings to assess **a.** prevalence of anthropogenic resources for avian scavengers, dogs, other commensals, and livestock; and **b.** prosocial or agonistic human and non-human animal interactions in shared space see (N. Kumar, Jhala, et al. 2019).

Ultimately, the usefulness of horizon scanning can only be judged retrospectively (Sutherland et al. 2019). Therefore, in **Stage 3**, the semi-structured and key-informant interviews were conducted to probe the social-ecological effects of urban opportunism by commensals as a surrogate for identifying major patterns in scavengers and vulture-specific perceptions in people, religion and occupation specific communities (abattoir and waste-workers), Non-Governmental Organisations (NGOs), government officials, and religious clerics. We conducted semi-structured interviews (n= 71) to identify how *extinction of experience* variably impacted people's perceptions and relationships with common avian scavengers-kites and house crows (details in Supplementary material 2). After vulture decline, these species exploit anthropogenic food and have attained extremely high population-densities in certain regions (Galushin 1971; N. Kumar, Gupta, et al. 2019). Based on information generated as part of this focused ethnography, we selected interviewees by snowball sampling after stratifying the potential respondents into various stakeholder units. We also interacted with professionals involved in animal husbandry, and with other wild or feral animals in shared urban space or zoological parks (Newing 2010). All interviews for **Stages 1 – 3** were conducted by the authors in *Hindi*, other native languages (*Bhojpuri*, *Maithili*, *Bengali*, *Assamese*) or English, as deemed appropriate.

Further, we compared descriptions about behaviour, appearance, role of culture and *extinction of experience* and grouped them into species specific themes (details in Supplementary material 1, 2). This focused study allowed us to cross-validate these thematic groupings and links between **(i)** political ecology driven by spatially-explicit social practices and activities that impact co-adaptations with urban nonhuman animals and **(ii)** individual-to-population scale feedbacks that characterise the urban ecology of opportunistic animals. For instance, it seems quite likely that before local extinctions, opportunistic consumption of carcasses by specific vulture populations attuned to settling within/near human-dominated landscapes inextricably tied their functional ecology with socio-economic practices (Fig. 2).

Based on ethnographic data, this manuscript tests the conceptual framework (Fig. 2) we developed for alterations in ethnoecology of human-animal interface, driven simultaneously by vultures' local extinction

and rapid urbanisation. For **Stage 4**, using this new conceptual framework, we aimed to critically evaluate the relevance of policies regarding the conservation breeding and restoration of vultures within or near human dominated landscapes in South Asia. We expected ecological salience for avian scavengers to be driven by our subjects' socio-cultural, professional and economic backgrounds, corresponding to regional socio-economic practices. Further, we expected the inductive-opinions embedded in folk-biology to accrue via direct encounters, which forms the basis of ecological, aesthetic and corporeal charisma (Lorimer 2007). Semi-structured interviews provided sufficient flexibility to identify patterns in avian scavengers' salience that we anticipated to be based on the age, profession, gender, and domicile.

2.1 Ethics statement

Approval for the semi-structured interviews, as part of ethnography, was granted by the Central University Research Ethics Committee (**CUREC**), University of Oxford (reference: SOGE 17A-82) and by the Training, Research, and Academic Council (TRAC) of the Wildlife Institute of India, Dehradun (WII). We conducted all interviews in accordance with the relevant guidelines and regulations and anonymity of respondents was ensured.

Results

3.1 Avian scavengers in socio-economic and socio-cultural systems

Amongst respondents, only the adults that aged more than 35 years recalled detailed descriptions about the appearance of vultures and their economic and cultural importance (supplementary material 1 and 2). Delhi was not the domicile for most of the subjects who witnessed large scavenging-flocks of vultures in the recent past. Timings of people's migration to Delhi (years 1980-2000), and *extinction of experience* regarding vultures' scavenging linked to animal husbandry practices based in villages/towns were strongly correlated.

Representatives from dairy colonies whose establishments are proposed to be shifted to north western part of the city in eastern Delhi discussed conflicts regarding disposal of animal waste and carcass. In the wake of vulture loss, situation of a vast number of such formal/informal dairy settlements that exist in Delhi and similar cities have been threatened (Baviskar 2020). Open spaces in cities, where immigrants within informal settlements and vultures drew mutual benefits from birds scavenging on carcasses of livestock that urban poor rear in their backyards have become scarce, precluding animal husbandry practices. People, especially males >35 years, whose work involved regular interactions with animals (municipality, zoological-park and NGOs working on animal welfare and conservation) shared relatively more direct experience, stories and knowledge about vultures and other avian scavengers, as compared to other stakeholders (summarised in Supplementary materials 1, 2).

Similar to how multiple morphological cues are used by taxonomists to classify and name a species, folk names, perceptions and practices associated with avian scavengers depended on locally prevalent folktales. Species-specific folk biology for avian scavengers was an outcome of long-term coexistence that cause humans and scavengers to modify their behaviours based on benefit trade-offs (details in supplementary material). For instance, cultural legends that explained avian scavengers' keen eyesight and flight capability captured peoples' inductive anthropomorphic opinions about physiological features that enabled synurbisation (Francis and Chadwick 2012). Folk biology was richest amongst urban poor within immigrant communities and/or livestock rearing. Anthropomorphism, therefore, linked local political economy and biophysical ecology of commensal avian scavengers in co-adaptations that are strengthened via behavioural reciprocations. Such co-adaptations that are driven by cultural geography extended the carrying capacity of urban ecosystems for select species (Fig. 2, 3).

3.2 Avian scavengers and "extinction of experience" after vulture decline

Anecdotes that people mentioned for direct vulture encounters invariably described village/locality-based carcass dumping areas carefully set aside from the residential blocks to harness their scavenging services (Fig. 1b). Depending on the financial status of the owner, in the absence of vultures that previously disposed livestock carcasses in urban as well as rural systems, carcasses are now often dumped in open water-bodies (canals or rivers), buried underground with salt, or discarded in open (see below). Livestock carcasses in Delhi are collected by the municipal workers, but only from the designated 'dairy-colonies', e.g., at *Ghazipur*. Thus, absence of vultures' services now spatially limits zones in cities where animal husbandry can be practiced by the urban poor. In their narratives, people frequently mentioned competitive release effects on stray dogs and rodents, and underscored heightened human-dog conflicts and threats of disease spread.

Homebound females and youngsters discussed the cultural salience of vultures, based on folktales, television-series and documentaries. While we attribute variations in perceptions about the same set of avian scavengers to cultural differences, all stakeholders concurred and justified explicit sympathy for the non-human life forms. All respondents shared that the motivation for keeping affiliative relationships with nonhumans came from the realisation that humans have destroyed and degraded natural habitats and wildlife has no option but to adjust with humans. It implied in people showcasing tolerance and care, even to species that are culturally looked upon with disdain, e.g., vultures. Universality of affiliative attitudes towards nonhumans across multiple local communities tied them in co-adaptations, wherein people frequently showcased religiously motivated empathy to wildlife.

Multiple raptor species that are facultative scavengers share similarity in plumage. Therefore, in people's responses, vernacular names for vultures and kites were used interchangeably (e.g., white backed vultures, Egyptian vultures and black kites; details in Supplementary material 2). Identifying raptors was a tedious task for subjects who were amateurs, considering major changes in plumage of raptors from juvenile to adult stage. Specific identification was further complicated in situations of sympatric opportunism exhibited by several such species on human-offal. At sanitary landfills in Delhi, which were

previously occupied by vultures until recently, large flocks of migratory black-eared kites *Milvus migrans lineatus* (n= 10,000 birds at *Ghazipur*. see (N. Kumar et al. 2020) are found. Co-occurrence of multiple avian scavengers on landfills/garbage likely contributed to misidentification of species.

Further, contrary to our expectations, immigrants who worked on waste over landfills, in close proximity of multiple avian and mammalian commensals, reflected poorly on ecological salience or charisma associated with scavengers. Their indifference to mega-congregations of kites and scarcity of opportunities to exhibit connections with biocultural heritage was likely an outcome of poor autonomy for the urban subalterns (Schell et al. 2021). Finally, the prevalence of ritualistic animal feeding and animal husbandry provided livelihoods to immigrants in Delhi.

Discussion

Our study offers clear examples of human-animal co-adaptations driven by complex cultural geography in tropics, wherein, stakeholder-specific economic activities and rituals are tied with functional ecology of urban species. In cities like Delhi, millions of animals from multiple wild, feral and domestic species that scavenge on waste also benefit from ritually offered food-subsidies by thousands of devout people who affiliate with non-human life forms. This tight human-animal interface - probably the largest in the world - is an integral part of South Asian urban-systems and culture (N. Kumar, Singh, and Harriss-White 2019). These human-animal interactions in tropical cities (Egerer et al. 2020), driven by people acknowledging age-old ecosystem services by animals, have configured regional urban nature-based-solutions for solid waste disposal (Hill et al. 2018; N. Kumar, Singh, and Harriss-White 2019; Strohbach, Warren, and Peterson 2014). Therefore, population declines in vultures that were keystone scavengers have impacted human activities and practices in addition to the direct effects on biogeochemical cycles (Estes et al. 2011). In particular, results from this study, which further contributes to the foundations laid by our prior research on population (N. Kumar et al. 2014; N. Kumar, Gupta, et al. 2018, 2019), behaviour (N. Kumar, Jhala, et al. 2019; N. Kumar, Qureshi, et al. 2018) and movement ecology of avian scavengers reinforces the call for (i) advancing the studies of human-animal interactions in tropical cities, and (ii) preferring transdisciplinary approaches to standalone ecological or ethnographic studies.

Overall, ethnographic surveys explained the roles people's beliefs and perceptions have in forming inextricable ties between cultural mosaics of multiple stakeholders and co-adapted urban biota (N. Kumar, Gupta, et al. 2019; N. Kumar, Singh, and Harriss-White 2019). Communities in cities within the Global South are conglomerates of human migrants from relatively rural areas. The SES framework (Fig. 2) as an outcome, therefore, contributes to designing and implementation of restoration policies for vultures and other wildlife within heterogeneously developed human dominated ecosystems, based on spatially-explicit human-animal co-adaptations (Athreya et al. 2018; Bhatia et al. 2021; Majgaonkar et al. 2019; Nair et al. 2021; Pooley, Bhatia, and Vasava 2021). The framework can help evaluate if target species for conservation and/or restoration can attain their erstwhile niche in the wake of urban changes and infrastructure development (Iaccarino 2003). For instance, vultures' access to food-subsidies would be impacted by urban-development in South Asia which entails increased power transmission lines. Such

impediments will continue to affect vultures and other large birds like Great Indian Bustard that frequently collide with windmills and/or electrocuted by overhead power lines (MOEFCC 2020). Based on our results, vulture restoration efforts in South Asia and developing tropical world would further be impacted by biocultural loss due to people, nature and culture dissociations (Miller 2005; Soga and Gaston 2016, 2020) as outcomes of rapid urbanisation. Biocultural loss affects citizens' attitudes and ecological salience for the non-human life forms as previously reported by (Celis-Diez et al. 2017)

Supporting the ecology of opportunistic synurbic organisms in tropical landscapes will need distinction in how we characterise 'cities' that are confined in political boundaries (Rademacher, Cadenasso, and Pickett 2019), unlike the far reaching social-ecological impacts of urban systems we found, which has previously been discussed by (Anonymous 2016; Klopp and Petretta 2017; Rees and Wackernagel 2008; Rosenzweig and Solecki 2001). When characterising organismic ecology well entwined with the populace, we need to account for the co-production of materials, information (tangible and intangible archives), people, and power relations to establish forms of interconnection that most meaningfully constitute the urban for humans and non-human lives in shared spaces (Adams and Hutton 2007; Folke 2006). Therefore, based on the following template consisting of population, demographic, behavioural and ethnoecological associations, we contextualise urban scavengers and people as co-adapting units in social-ecological systems (SES) (Bergsten, Galafassi, and Bodin 2014; Folke et al. 2005; Ostrom 2009; Tidball and Stedman 2013).

First, as a top-trophic raptor with large home ranges, vultures fall under those avian groups that successfully colonised and thrived in human-dominated landscapes, attracted to the frequent allocation of anthropogenic resources (Monsarrat et al. 2013; Vasudeva 2021). Raptor populations are typically limited by food and nest-sites (Newton 1979), wherein, the latter constrains the level of resource-tracking by individuals attuned to opportunism (e.g. (N. Kumar, Gupta, et al. 2019)). However, unlike the commensal-scale urban niche for kites and crows, vultures' services were resolutely harnessed by locals through the allocation of designated feeding sites - an age-old practice in South Asia analogous to today's "vulture-restaurants" (Arkumarev et al. 2021). It not only had implications for solid waste and disease management but also supported the world's largest livestock population in poverty-stricken regions (Botha et al., 2017; Livestock Census of India, 2019; MOEFCC, 2020). Right until the last century, this vulture-mediated nature-based-solution for solid waste disposal simultaneously addressed economic, sustainability and socio-cultural goals.

There is great diversity in the current status of vultures in their distribution ranges across the world, driven by regional differences in social motivations and perceptions for nonhuman lives co-adapted to regional communities (Botha et al. 2017; MOEFCC 2020; Prakash et al. 2003; Pritchard 2020). Consequently, based on our results for the Indian subcontinent's urban future, the largest milk-producing region of the world, we reckon coupling: **(i)** dairy-colonies' displacement that is part of urban gentrification drive (DDA 2017; Dutta and Bandyopadhyay 2011); and **(ii)** release of captive bred vultures from conservation-breeding facilities like *Pinjore*, Haryana (India) (MOEFCC 2020; Prakash et al. 2003). The latter would depend on careful, multi-stakeholder and multi-scalar planning (Williams, Balmford, and Wilcove 2020) to

afford accessibility of safe feeding, roosting and nesting sites for vultures, whose services could easily be exploited as a tool to simultaneously address urban waste and poverty (N. Kumar, Gupta, et al. 2019; N. Kumar, Singh, and Harriss-White 2019). For instance, north-western Delhi, where informal livestock-rearing colonies' resettlement is planned (DDA 2017; Dutta and Bandyopadhyay 2011), lies in proximity to the *Aravallis* range that is currently an active, safe nesting zone (Authors' unpublished data).

Correspondingly, policies pertaining to vulture restoration shall solicit simultaneous contributions from the federal and Non-Governmental Organisations (NGOs) that concern the maintenance of environment and forests, animal husbandry practices and resettlement of the urban poor.

Second, the demographic shifts in vulture populations accompanied changes in human population structure across the globe, especially in the Global South (Census Organisation of India, 2011; (United Nations Population Division 2018)). We found that migration to cities selectively de-couples younger generations from the joint-families (e.g. see Gosler and Tilling 2021), disrupting direct and oblique biocultural transmissions. Our results inform that transgenerational prevalence of affiliative attitudes to animals in shared environments formed the basis for mutual tolerance (Fogarty, Creanza, and Feldman 2019; Majgaonkar et al. 2019; Nagendra 2018). Cities' physical urban sprawl and far-ranging social-ecological footprint will likely limit success of vulture-reintroduction. Therefore, demographic repair for vultures should factor in socio-cultural dynamics in urban communities in ways that support re-attainment of co-adaptations that are conducive for ecosystems that are now urbanised (Fogarty, Creanza, and Feldman 2019; Lieury et al. 2015).

Third, while interviewees shared deep insights about religious beliefs that motivated them to exhibit affiliative behaviour and tolerance for animals including vultures in localities, unfortunately, we have no records of how vulture breeding-pairs dealt with the behavioural bottleneck of nesting in human dominated landscapes. These bottlenecks for vultures and other urban fauna involve benefit trade-offs in urban environments in terms of defending their young against humans, while exploiting anthropogenic food sources (N. Kumar, Qureshi, et al. 2018). Recent studies on birds that occupy and exploit anthropogenic resources have discussed animal-personalities attuned to the higher-end spectrum of urban life via selection of opportunistic individuals (Bókony et al. 2012; N. Kumar, Gupta, et al. 2018; Miranda et al. 2013). But unlike multiple birds that have been studied to aggressively attack human beings while defending offspring, e.g., kites (N. Kumar, Jhala, et al. 2019), and magpies (Jones and Thomas 1999), vultures are not known to attack humans (Ferguson-Lees and Christie 2001; Naoroji 2007; Schell et al. 2021). Therefore, we speculate that vultures-populations breeding within cities were constituted by individuals that had synurbic personalities, developed via selection for tolerance to human proximity as a behavioural strategy (N. Kumar, Gupta, et al. 2019; N. Kumar, Jhala, et al. 2019).

This urban opportunism was also the basis for ecological trap (Schlaepfer, Runge, and Sherman 2002) that fuelled rapid decline of vulture populations that consumed cattle-carcasses which had diclofenac-residues (Prakash et al. 2003). Contextualising the niche of avian-scavengers conjugated with animal-husbandry practices, behavioural-phenotype(s) (Stephens and Sutherland 1999; Sutherland 1998) of the captive-bred vultures - often collected from protected areas (MOEFCC 2020) -might preclude their

settlement in modern day human-use landscapes. We predict that such small vulture populations will be exposed to threats of human-persecution like Africa (Botha et al. 2017), due to socio-demographic shifts in urban populace that we studied in relation to the cultural tolerance for avian-scavengers (Cantor et al. 2021; Mbizah et al. 2020; Sutherland 1998). Alternatively, urban opportunism on cattle carcasses could have been species-specific tolerance of proximity to humans, selecting for White-rumped vultures *Gyps bengalensis* that constituted >80% of all vultures in South Asia before they declined (MOEFCC 2020; Prakash et al. 2003). Decoupling of human-vulture co-adaptations by the turn of the last century has contributed to a long-drawn social-ecological trap (Haber 2007). Further, anthropomorphic socio-cultural legends discussed by people were popularised by social and televised media. In addition to enabling communities in upholding their affiliative attitudes to urban animals, media also spread misinformation about causes for decline vultures, occasionally vilifying them as bad omens. Such fake news and socio-cultural shifts can affect the existing small populations as well as reintroduced vultures (Margalida and Donazar 2020).

Fourth, according to the SES framework (Fig. 2), bi-directional feedbacks link aforementioned perspectives on population, demographic and behavioural domains for the human-animal co-adaptations. In Delhi, these dynamic ties characterised regional variations in ethnoecology of tropical urban ecosystems (Almada 2011; Johnson and Hunn 2010; Sarmiento 2005). For instance, previous studies (Lamb et al. 2020; Nyhus 2016), including a few in the region (N. Kumar, Gupta, et al. 2018; N. Kumar, Qureshi, et al. 2018), have shown that commensal species' functional ecologies are ascribed via centuries of coexistence, enabling metabolism of human offal by opportunistic species at multiple trophic levels. Food waste is a valuable subsidy to livestock and poultry owners in South-Asian cities and towns (N. Kumar, Singh, and Harriss-White 2019). The urban ecology of the human-animal interface in developing systems entails selection of informal livestock rearing practices. These ethnic-practices sustain and support millions of urban poor and configure regional political economies and ecologies, with respect to select animal species that successfully cohabit (Chan, Satterfield, and Goldstein 2012). Along with sharing living spaces with commensals, in Delhi, people within informal-colonies kept livestock that subsist on edible waste as nutrient-rich feed in backyards. This practice, which is quite prevalent across the developing world, reduces the costs of milk and meat production (Allievi, Vinnari, and Luukkanen 2015; Salemdeeb et al. 2017; Speedy 2003). Further, scavengers like vultures, dogs, kites, rats and crows consume the organic remains in shared spaces. Across the developing world - specifically in South Asia - commensals survive via spatially explicit co-adaptations, with highly variable synurbic status (Francis and Chadwick 2012). Therefore, for the old world, the fastest declines witnessed in the vulture populations should not be treated as an event isolated from changes occurring simultaneously in the human-wildlife interface and socio-economy. Such events are driven by, and, in turn, further cascade urban growth and development that shapes local culture, built environment and social-ecological processes (Allievi, Vinnari, and Luukkanen 2015; Steinfeld 2004). Furthermore, tropical cities have witnessed massive increase in their solid waste since the vulture decline e.g., Delhi's waste grew by 300% since 2002 (Talyan, Dahiya, and Sreekrishnan 2008). Unlike their western counterparts, the ecology of human-nature interactions in tropical megacities (Soga and Gaston 2020) respond to the geography of

human religion, hygiene and poverty. Availability and accessibility to garbage as food subsidies affects non-human life forms via interactions between socio-economic and socio-cultural processes that have altered social-ecological processes from micro-habitats to landscapes (Fig. 4) (Folke et al. 2005).

Moving on, vultures' loss has had its share in contributing to the burden of diseases that spill from animals to humans (zoonoses) (Markandya et al. 2008), often due to the competitive release effects on mammalian species, e.g., stray dogs, macaques and rats that are part of urban scavengers' guild. In South Asia and Africa that have the highest zoonotic burden (Grace et al. 2012; Markandya et al. 2008) reintroduction of vultures will be impacted by impending competition over anthropogenic food-subsidies (N. Kumar, Singh, and Harriss-White 2019). Considering the perpetual increase in solid waste and its poor disposal in South Asia (Joshi and Ahmed 2016; S. Kumar et al. 2017) that supports dense populations of free-ranging animals, successful proliferation of captive-bred vultures will be challenging. These challenges would emanate from the projected urbanisation of 500-million citizens within the Indian subcontinent over the next 30 years (Anonymous 2016; Folke et al. 2005; Levin et al. 2013; McDonnell and MacGregor-Fors 2016; United Nations Population Division 2018).

Finally, while vulture species across the world face immense threats, a comparison of their current precarity in Asia, Europe and the African continents (see Table 1) reflects the diversity in socio-cultural and economic issues, for which we reckon spatially-explicit policies that factor regional ethnoecologies (Williams, Balmford, and Wilcove 2020). For Afro-Asian landscapes, challenge of vulture conservation invariably involves agroecosystems interfacing the protected area systems (Karanth and DeFries 2011). Within Europe and Africa, illegal use of poison baits is the most important human-induced factor for local extinction or decline in vertebrate megafauna, including Red Kites and Vultures (Margalida 2012; Margalida et al. 2010). Additionally, vultures are vilified in many regions in Africa, from where studies have not reported ethno-ornithological beliefs and practices that still motivate people to maintain affiliative relationships with vultures and other avian scavengers (N. Kumar, Gupta, et al. 2018; N. Kumar, Jhala, et al. 2019; N. Kumar, Singh, and Harriss-White 2019), as reported Taneja (2015). Hence, successful vulture reintroductions in the Global South would invariably be tied with urban planning that upholds human-animal co-adaptations that involve payoffs for both agencies (Adams and Hutton 2007; Folke 2006; Folke et al. 2005; Smit and Wandel 2006; Walker 2005, 2006; West 2005).

Table 1: A comparison matrix of current conservation threats, policy tools for vultures in Asia, Europe and the African continents, and the impacts of regional losses reflects the distinguishable socio-cultural as well as socio-economic factors for respective regional ethnoecological practices. Adapted from CMS Raptor MOU Technical Publications (Botha et al., 2017; Pritchard, 2020)

Region	Vulture spp	CR Status	Major Policy intervention	Socio-cultural, persecution status	Threats	Impact of vulture loss	References
Asia	Bearded Vulture <i>Gypaetus barbatus</i>	NT		belief based persecution in Nepal	persecution, decline in food availability	increase in population of mammalian scavengers like dogs, genetic bottlenecks	(Acharya et al. 2010)
	Egyptian Vulture <i>Neophron percnopterus</i>	EN	Ban on diclofenac		electrocution, NSAID poisoning		(Al Fazari and McGrady 2016; Galligan et al. 2014)
	Red-headed Vulture <i>Sarcogyps calvus</i>	CR		reported in Cambodia	NSAID poisoning, habitat loss, electrocution		(Naidoo et al. 2009)
	Himalayan Griffon Gyps <i>himalayensis</i>	NT		reported in Cambodia	NSAID poisoning, habitat loss, electrocution		(Green et al. 2004)
	White-rumped Vulture Gyps <i>bengalensis</i>	CR		reported in Cambodia	NSAID poisoning, habitat loss, electrocution		(Cuthbert et al. 2016)
	Indian Vulture Gyps <i>indicus</i>	CR			NSAID poisoning, habitat loss, electrocution, unintentional poison baits		(Cuthbert et al. 2016)
	Slender-billed Vulture Gyps <i>tenuirostris</i>	CR			NSAID poisoning, habitat loss, electrocution, unintentional poison baits		(Cuthbert et al. 2016)
	Griffon Vulture Gyps <i>fulvus</i>	LC		reported in Cambodia	NSAID poisoning, habitat loss, electrocution, unintentional poison baits		(Cuthbert et al. 2016)
	Cinereous Vulture <i>Aegypius monachus</i>	NT	ban on diclofenac	persecution for feathers	unintentional poison baits, electrocution, decline in food availability, NSAIDS, persecution		(Batbayar N., Tseveenmyadag, N., Kee, P. W. and Lee 2005; Dixon et al. 2013)
	Lappet-faced Vulture <i>Torgos tracheliotos</i>	EN			insufficient data		

Africa	Bearded Vulture <i>Gypaetus barbatus</i>	NT	research and policy decision in making		Unintentional poisoning (baits), collision with powerline, lead poisoning	genetic bottlenecks	(Krueger et al. 2014)
	Egyptian Vulture <i>Neophron percnopterus</i>	EN			Unintentional poisoning (baits), collision with powerline, decline in food availability		(Angelov, Hashim, and Oppel 2013)
	White-headed Vulture <i>Trigonoceps occipitalis</i>	CR		intentional poisoning	poison baits, sentinel poisoning, habitat loss, decline in food availability		(Buij et al. 2016; Roxburgh and McDougall 2012)
	Hooded Vulture <i>Necrosyrtes monachus</i>	CR		persecution for wildlife parts	bushmeat trade, poison baits, sentinel poisoning		(Buij et al. 2016; Rondeau and Thiollay 2004; Roxburgh and McDougall 2012)
	White-backed Vulture <i>Gyps africanus</i>	CR		persecution for wildlife parts	poison baits, sentinel poisoning, habitat loss, decline in food availability, electrocution		(Steven McKean et al. 2013; Roxburgh and McDougall 2012)
	Cape Vulture <i>Gyps coprotheres</i>	EN		belief based use-African Traditional medicine	poison baits, electrocution		(Diekmann and Strachan 2006; S McKean and Botha 2007; Pfeiffer and Ralston-Paton 2018)
	Rüppell's Vulture <i>Gyps rueppelli</i>	CR		belief based use-African Traditional medicine	poison baits		(Buij et al. 2016; Kendall and Virani 2012)
	Griffon Vulture <i>Gyps fulvus</i>	LC		belief based persecution			
	Cinereous Vulture <i>Aegypius monachus</i>	NT					found occasionally
	Lappet-faced	EN		belief	poison baits,		(Groom et al.

	Vulture <i>Torgos</i> <i>tracheliotos</i>			based use	habitat loss and disturbance, sentinel poisoning		2013; Kendall and Virani 2012; Ogada, Botha, and Shaw 2016; Shobrak 2011)
Europe	Bearded Vulture <i>Gypaetus barbatus</i>	NT	vulture feeding sites; research and policy decisions on powerline collision and poisoning underway		Unintentional poisoning (baits), collision with powerline, lead poisoning	genetic bottlenecks	(Berny et al. 2015; Margalida et al. 2008; Mateo et al. 2015)
	Egyptian Vulture <i>Neophron percnopterus</i>	EN			Unintentional poisoning (baits), collision with powerline, lead poisoning		(Donázar, Cortés-Avizanda, and Carrete 2010; Saravia et al. 2016)
	White-backed Vulture <i>Gyps africanus</i>	CR			-		found occasionally
	Rüppell's Vulture <i>Gyps rueppelli</i>	CR			-		found occasionally
	Griffon Vulture <i>Gyps fulvus</i>	LC			Unintentional poisoning (baits), collision with powerline, NSAIDs		(Ferguson-Lees and Christie 2001; Prinsen et al. 2011)
	Cinereous Vulture <i>Aegypius monachus</i>	NT			decline in food availability		(Moreno-Opo et al. 2010)

In summary, poor prevalence of religiously motivated affiliative attitudes for commensals in youngsters (N. Kumar, Gupta, et al. 2018)- a generational shift we noticed via ethnography- will eventually alter tolerance for backyard-biodiversity. In the near future, progressive loss of biocultural diversity for backyard species will further homogenise human perceptions and attitudes for vultures across the old world (Donázar et al. 2009; Margalida et al. 2010). Thus, we expect further vilification of vultures and other avian scavengers that may lead to increased cases of indirect poisoning of avian scavengers over depredated cattle carcasses laced with organochlorides to avenge the livestock-loss caused by mammalian carnivores (Hernández and Margalida 2009; Oaks and Watson 2011). We base this argument on the exposition of relatively small protected areas (average size = 486 km²) (Karanth and DeFries 2011) that increases their interface with agroecosystems witnessing rapid loss in tolerance for wildlife in South Asia (Clark et al. 2013; Watson et al. 2014). In the wake of urban changes that entail habitat fragmentation and biocultural loss, a general increase in agonistic attitude towards wildlife (Rodgers, A., Hartley, D., & Bashir 2003) is expected to spill over to vultures in South Asia (MOEFCC 2020).

Therefore, restoration for vultures and other wild fauna would require holistic policies that incorporate policies that adhere to the SES framework we propose for tropical megacities. It should inculcate a nuanced understanding of spatial variations in ethnoecological attitudes for the non-human organisms; an approach that is analogous to patch dynamics in ecology (Abel, Cumming, and Anderies 2006; Pickett et al. 2001).

Conclusion

In conclusion, the SES framework as the outcome of this study models the contingency of biodiversity conservation in the human-dominated landscapes on ecological as well as social, cultural and economic factors. The loss of vultures quintessentially depicts how limited social-ecological understanding delayed actions on the conservation and management of a once-common group of species. For poverty-stricken urbanising ecosystems of the developing world, we cannot afford to overlook the human factors that govern criterion of habitat selection by opportunistic animals. Urban ecology of commensals is contingent on food-affording socio-economic drivers and cultural beliefs at the local to regional scales. Therefore, integrating human socio-cultural estimates while releasing animal individuals during restoration practices would affect population-level behavioural consequences and back, via bidirectional feedbacks (Cantor et al. 2021; Mbizah et al. 2020). In turn, progressive rationalisation of refuse disposal and detachment of younger generations from ritual practices and beliefs, which modulate tolerance for non-humans, make wildlife restoration a moving target within developing countries. Conservation efforts need to cater to conundrums between modernisation and improving human living conditions while upholding ecological and cultural salience for non-humans in ways that preclude attainment of social-redundancy for target species like vultures.

Declarations

Acknowledgements

Discussions during the PAWS-Web Network's (www.PAWS-Web.site) workshops (India-Oxford Initiative's GCRF fund AT13.01) helped design the framework we proposed and tested in this study. The FCO Chevening-HSBC Scholarship, and grants from the University of Oxford (Hansell Travel and Discretionary-Grants from Somerville College, and Dissertation-grant of SoGE, and Felix Scholarship), the Raptor Research and Conservation Foundation, Mumbai, and the Govt. of India's MoEF&CC provided funds. Delhi's Police, Forest Department, municipal corporations and civic bodies gave permits. Maan Barua supervised UG's M.Sc. thesis and Yadvendradev V Jhala, Qamar Qureshi, Andrew Gosler and Fabrizio Sergio supervised the "Black Kite Project". We thank Laxmi, Prince, Zehen, Aparajita, Harsha, Poonam, Navneet, Abhinandan, Ameer, Navneet, Prashant and Gunjesh for fieldwork. Delhi citizens and officials at the Wildlife Institute of India extended support. Trevor Price, Bornika Roy, Ujjwal Kumar and Pariva Dobriyal reviewed previous drafts.

Author Contributions

UG conducted the focal interviews of 71 focal-subjects in 2017 and prepared a preliminary draft for the partial fulfilment of her M.Sc. thesis at Oxford. Both the authors designed the study, conducted fieldwork between 2012-2021, wrote this manuscript and approved the final version.

Conflicts of Interests

The authors declare no conflict of interest. The funding agencies had no role in the study design and fieldwork.

Data availability statement: Apart from the supplementary files, additional archivable data will be available at Oxford University's Research Archive (ORA).

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Figures

Figure 1

Methodological stages (adopted and modified from Esmail et al. 2020) illustrating how people involved in opportunistic surveys and focused ethnography participated at each stage of assessment for human-animal co-adaptations. Assessors are the paper's authors.

Figure 2

The social-ecological system dynamics in tropical ecosystems shared between humans and opportunistic animals via co-adaptations (adopted and modified from (Gómez et al. 2016)), consisting of non-human populations (exemplified here with avian scavengers) is driven not only by the ecological processes, but it also closely responds to people recognising the concerned specific ecosystem services in the form of social perceptions and salience. Conversely, socio-economic and cultural processes of human systems within landscapes shared with diverse populations of non-humans is linked to ecosystem services of select species that contribute to human well-being. The ethno-ecological systems thus formed are an outcome of centuries of coexistence. Given the mutual interactions, this study tests how two bi-directional feedback loops should be the fulcrum of wildlife restoration for species like vultures in South Asia.

Figure 3

Cyclical ecosystem-based framework to represent one of the many community-governed social-ecological-systems (Ostrom 2009) during the last century in South Asia. The framework links the a. nature based solutions for waste management by opportunistic scavengers, including vultures, in shared living spaces; b. Social-cultural and socio-economic aspects associated with carcass disposal by vultures and involvement of specific stakeholders from certain caste (Chamars) and religion (Muslims) involved in leatherwork; and c. Balancing of stigma for vultures through socio-cultural legends, where mythological references (in Ramayana) for vultures' volant capabilities and keen sense of sight are topics of reverence, forming the bases for mutual tolerance in the region. This conceptual framework builds on the non-human charisma and salience discussed by Lorimer (2007) and illustrates why the ecology of human-nature interaction in temperate systems differ from tropical human-use landscapes (Soga and Gaston 2020).

Figure 4

Cyclical ecosystem-based framework concerning human-vulture interface has attained novel status in the wake of South-Asian quasi-extinction of vultures through: a. Gentrification driving loss of nature based solutions that decreases people's motivation for sharing living spaces with animals in a tropical urban landscape; b. Spatio-temporal correlations in urbanisation and vulture loss has been impacting the social-cultural and economic aspects that now mediate competitive release of other commensals competitors

that capitalise on carcasses left or buried within limited spaces; and c. the loss of direct encounters of due to rapid changes in demographic parameters of vultures and humans that shared urban areas. Access to television and internet impacts biocultural heritage and spreads mediatized misinformation about their local-extinction due to “technology-assisted” migration to Japan and USA. The broken red lines represent how vulture loss has affected the cyclic relations for the non-human charisma and salience involving vultures (Lorimer 2007). Overall, the impacts on cyclicity have led to changes in livestock maintenance for animal protein and leather, depicted in the section d. that represents how urban practices across the world are getting homogenised in space and time.

Supplementary Files

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