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Cultural practices and food subsidies shape the architecture of multispecies coexistence in a tropical megacity

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Abstract

1. Multispecies relationships among people and nature in tropical cities are increasingly shaped by pervasive waste systems, against the backdrop of changing cultural practices and infrastructure. But human–animal conflict is often managed through reactive, species-specific interventions that overlook the social-ecological processes producing urban coexistence. We examined how cultural practices and food subsidies structure coexistence in Delhi, focusing on free-ranging dogs (FRD), rhesus macaques and black kites as ground-dwelling, arboreal and aerial commensals exploiting the human niche at different spatial and temporal scales.

2. We integrated quantitative ecological surveys, a management-intervention case study, long-term black kite research and coexistence observations across 1500 km^2 of Delhi. For FRDs, we conducted photographic capture–recapture surveys across 14 stratified sampling units covering 2.95 km^2, ecology and the distribution of food subsidies. For macaques, we documented recolonisation following the translocation of ~50 individuals from a university in Delhi. These ecological observations were interpreted alongside semi-structured interviews (n=65) and long-term ethnographic research.

3. Delhi supported an estimated 795,313 dogs, with a mean density of 530±89 dogs/km^2. Surveyed neighbourhoods contained an estimated 218±51 feeding stations and 57±16 garbage accumulation points per km^2. Dog pack density was strongly associated with feeding infrastructure. Macaque numbers at the university campus returned to pre-intervention levels within one month, indicating rapid recolonisation where ecological conditions and resources persisted. Long-term kite research showed stable breeding densities and large landfill aggregations linked to ritual meat provisioning and refuse availability. Ethnographic findings revealed that conflict vulnerability was unevenly distributed, with outdoor workers and socioeconomically marginal groups bearing disproportionate exposure while possessing limited management agency. Cultural ambivalence toward ritual feeding—simultaneously expressing spiritual obligation and conflict concern—defied simplistic prescriptions.

4. Across taxa, coexistence was shaped not simply by animal abundance, but by how human-derived resources were organised in space, time and culture. Feeding fostered mutual recognition and conflicts, varying at scale, from individuals (dogs) to groups (macaques) and populations (kites). Coexistence management requires shifting from species control towards relationship management: modifying feeding practices, waste infrastructure, built infrastructure and stakeholder participation to address the conditions through which multispecies cities are continually produced.

Key words: Urban ecology; Human-wildlife conflict; Anthropogenic food subsidies; Environmental justice; Social-ecological systems; Commensalism; South Asia; Behavioural adaptation; Animal welfare; One Health

1. A fictional prelude: Delhi, 2030

Hello! *Cities like Delhi did not choose multispecies coexistence, unlike their western counterparts where its aspects are typically and consciously planned/designed. Delhi became one through regional social agglomerations of habits, beliefs, faith, waste, tolerance, neglect, and their complex, cyclical feedback of virtues and vices. Ground dwelling animals in tropical cities have to tread rapidly changing streets. Arboreal fauna like monkeys learn to scale built infrastructure amidst trees. And opportunistic scavengers like kites are associated with markets, landfills and ritual feeding sites. Most distinctively, people are woven in tropical urban ecosystems as companions, less custodians. Albeit, it is changing rapidly amidst threats, omens, and nuisances/disease risks from animals. The latter developments have necessitated municipal interventions as developing cities endeavor to achieve "global standards".*

In 2030, these relationships are fractured. Shared spaces that once depended on informal tolerance have become accusation arenas. Dog/monkey feeders, bite victims, municipal agencies, animal advocates, sanitation workers, commuters and resident welfare associations have frequently conflicting priorities. Local removals now provoke counter-mobilisation, with occasional cases of poisoning incidents, polarising the public. While certain stakeholders defend sheltering and sterilisation as humane interventions, others rejected these measures as inadequate, cruel, or ecologically naive. I suggest that apparent "problems" of dogs, monkeys or birds is in fact a deeper, systemic failure: the collapse of shared interpretive worlds. South Asian cities are fast becoming unfamiliar for humans and animals alike, and serve the interests of a privileged minority.

For instance, Delhi's streets are dense information landscapes. Dogs read human posture, feeding routines, traffic rhythms, territorial scent, vocal cues and the responses of other dogs. Macaques follow specific routes to access food and shelter, navigating progressively shallow human tolerance. Altered refuge/escape routes and intensified religious provisioning further create confusion. Kites read air currents, refuse pulses, nesting substrates, human movement and the predictability of ritual feeding to settle. Humans, in turn, read these animals through fear, familiarity, religion, caste and class position, public-health narratives, personal memory and policy categories. Coexistence persists when these cue–outcome relationships remain interpretable. Conflict escalates when they become noisy, contradictory or unintelligible.

Wildlife management in the tropical cities operates on assumptions that animals perceive interventions as intended. Translocated macaques are expected to remain where released. Sterilisation and feeding of street dogs have long been suggested to make them less conflict-prone, expectedly reducing bites/rabies. Nonetheless, the dystopia Delhi and similar cities are experiencing in 2030 is preventable, which requires a science of tropical cities: one that bridges behaviour, ecology, culture, disease risk, infrastructure and governance priorities without reducing coexistence to either sentiment or control. In addition to building datasets on where animals are, how many exist, or what resources sustain them, we must ask whether we can effectively integrate Western urban infrastructure with regional mindsets of coexistence in tropical urban environments.

The poem below is a deliberate, non-standard descriptor of multispecies coexistence. It is not offered as evidence, but an orientation—a reminder that coexistence is experienced before it is measured. Researchers must ask a narrower question: *how do cultural feeding practices and urban waste systems shape the ecology of non-human denizens in Delhi*? Through this question, urbanites could examine a broader proposition: that multispecies coexistence in tropical cities depends on how human-derived resources, cultural practices and information landscapes remain interpretable across species.

In the heart of many tropical cities, where the concrete meets the sky,
Quadrupeds (ground-dwelling) meet bipeds (humans) in a dance to comply.
A constant cognitive mutualism, familiar and yet new,
With barks, whines, and tail wags, their signals are true.

Negotiating streets, amidst the urban beat,
A dance of coexistence, where different life worlds meet.
For what dogs or coyotes consider safe, humans may not agree,
Yet they continue to negotiate, in the city, as we see.

'Tailed Simians' in their realm, brachiate with grace,
From branch to branch, they find their (limited) urban space.
Meeting humans in the streets, when safety/food is assured,
Yet the dynamic streets often bring discord.

And then there are avian scavengers, soaring high and free,
Over unfamiliar turf, as far as their eye can see.
Hostilities arise, but only for a time so brief,
When parent-birds are tied to nests, intrusion brings grief.

Birds negotiate with winds in the tropical city's core,
Finding conducive spaces, forever exploring more.
This is the code of coexistence, a lesson to be learned,
In the heart of the city, where many 'lifetables' are turned.

From ground dwellers to arboreal, to aerial lifestyles wide,
The spectrum of human-animal negotiations, side by side.
It is a dance of life, a symphony bitter yet sweet,
In the urban jungle, where different life worlds meet.

Yet, in this dance, there is a tropical rhythm, a beat,
Shaped by Eastern religions, cultures, and the streets.
Known to prevent indiscriminate culling, retaliation's tide,
When some animals become threats to urban pride.

This cultural essence of coexistence, this cognitive dissonance,
Potentially allows Indians to protect their biodiversity with such resonance.
It is not always about wisdom, not always about scientific discourse,
But about living together, coexisting, and staying the course.

But there is a modern prevalence, a non-traditional patronising tone,
Towards non-human city dwellers, opportunistic ones full-grown.
Ritually fed by people, a practice spread wide,
Might not be justified—it is a dangerous ride.

Subalterns in humans and animals both bear the heaviest cost,
When the web of interdependence is lost.

Because of fear of conflicts and diseases animals spread,
which affects the subalterns, more exposed to such dread.
Thus, warranting scientific evaluations, a need to reassess,
Traditional practices once ensured coexistence progress.

2. Introduction

As human habitats and habits transform in the 21st century (Anonymous, 2016), relationships between people and urban-adapted animals are being reconfigured at unprecedented rates (Nyhus, 2016). This is especially evident in tropical cities, where rapid urban expansion, dense human settlement, uneven development and long-standing cultural practices of provisioning animals intersect within shared landscapes (Gupta & Kumar, 2024; Kumar et al., 2019a,b). Urban centres now shape some of the most consequential encounters between people and nature, yet the social-ecological processes through which coexistence is maintained, disrupted or transformed remain insufficiently understood (Soga & Gaston, 2020). It is expected to deteriorate and skew further, with approximately 65% of humanity now dwelling in cities occupying less than 4% of Earth's land area (UNO, 2018). This crisis of multispecies coexistence depicted in the opening fictional narrative from 2030 reflects how expanding urban features within tropics demand immediate attention.

The fact that urban animals do not passively occupy built environments is a central coexistence challenge; they exploit human-derived resources that are themselves socially and culturally organised (Kumar et al. 2019c). Food subsidies produced through household feeding, ritual provisioning, slaughterhouse waste, markets and refuse disposal create resource landscapes that differ in spatial distribution, temporal predictability and accessibility. These subsidies frequently sustain enormously high animal densities, alter movement and foraging behaviour (Kumar et al., 2014, 2019c), and generate repeated and predictable encounters with people (Bhattacharjee et al., 2018; Bhattacharjee & Bhadra, 2022). However, their effects are unlikely to be uniform across taxa. Ground-dwelling, arboreal and aerial commensals experience the same city through different bodily capacities, spatial constraints and forms of access to human resources. In fact, the social perceptions in localities play a major part in how some of these species become cultural keystones (Gupta & Kumar, 2024). Understanding coexistence therefore requires asking not only whether animals use anthropogenic subsidies, but how the organisation of those subsidies shapes different architectures of human-animal relationship.

South Asian cities provide a crucially important context for examining this problem. Ritual feeding of urban commensals—including dogs, macaques, kites and cows—is prominent in many Indian traditions and may reflect long-standing ethical and religious commitments to multispecies coexistence (Kumar et al., 2019c; Pinault, 2008). At the same time, these practices now interact with expanding waste systems, informal labour, public-health anxieties and increasingly reactionary management interventions (Evans & Gawlik, 2020). Urban refuse and direct provisioning together produce heterogeneous mosaics of habitat suitability, especially in cities where solid waste management remains poor and uneven, and animal scavenging is implicitly incorporated into everyday sanitation systems (Kumar et al., 2018a; 2019a,b,c). These interacting tangible and intangible conditions make tropical urban ecosystems distinct from the temperate and Western systems that have dominated much urban ecological theory (Evans & Gawlik, 2020; Oro et al., 2013).

Despite growing research on urban wildlife, three vital gaps remain under addressed. ***First***, tropical urban systems remain underrepresented in comparative urban ecology, despite containing dense multispecies assemblages shaped by rapid infrastructural change. ***Second***, studies often examine population size, conflict or management in single-species terms. Such simplistic approaches leave the shared social-ecological mechanisms—linking human practices, animal behaviour and urban infrastructure—insufficiently resolved. ***Third***, cultural feeding and waste systems are often treated as background conditions rather than modifiable ecological processes that structure behavioural and population dynamics, encounter patterns and management outcomes (Fall & Jackson, 2002; Gil-Fernández et al., 2020; Kokko & Sutherland, 2001; Wong & Candolin, 2015).

Here, we address these gaps to characterise tropical urbanism through a comparative study of commensals in Delhi. We focus on three taxa that represent contrasting modes of adherence with the human niche, which enable resource exploitation: FRDs as ground dwelling, rhesus macaques as arboreal exploiters and black kites as aerial scavengers. These taxa differ in mobility, social organisation, dependence on anthropogenic resources and the forms of human-animal conflict they generate (Gámez & Harris, 2022; Hussain & Baumann, 2024; Pocheville, 2015; Regos et al., 2021). Rather than treating them as separate case studies, we use them as complementary expressions of a common process: subsidy-mediated coexistence in a tropical megacity. Detailed species background, including their ecology, management challenges and evidence gaps, is provided in Supplementary Material S1.1.

This paper examines how cultural feeding practices and urban waste systems are shaped by, and, in turn, further shape the ecology and human experience of urban commensals across guilds Kumar et al. 2019c). Specifically, we studied how differences in subsidy distribution, predictability and accessibility influence population persistence, spatial aggregation, recolonisation and patterned encounters with people. We integrate quantitative ecological data on FRDs, a macaque displacement case study and long-term black kite research with ethnographic observations of human-animal relationships. Through this comparative framework, we examine how co-cultural relationships at the human-animal interface are maintained or destabilised under contemporary tropical urbanism.

We argue that coexistence in such systems is not merely a question of animal abundance or human tolerance. It emerges through the organisation of resources, built form, cultural practice and repeated information exchange between humans and animals. Feeding practices and waste management systems are therefore not peripheral to urban ecology; they are ecological infrastructures through which multispecies cities are continually produced. Because these systems can be modified through policy, design and community engagement, understanding their ecological consequences is essential for moving beyond reactive, species-specific interventions towards more predictive and equitable approaches to urban coexistence.

Urban centres, thereby, have become the determinants of, and shall further shape, people and nature relationships, affecting coexistence. The challenge of reconciling cross-species associations, developed via long-drawn coexistence recently termed co-cultures (Sueur & Huffman, 2024) is facing novel challenges. Heterogeneous and poorly planned infrastructure expansion in developing tropical regions like South Asia alters people and nature’s relational consistency. Further, biotic communities centered around humans in cities like Delhi have pressures from shifting cultural practices that converge in social-ecological conglomerates, creating tensions with management approaches (Kumar et al., 2019c).

Waste-full urban expansion, invariably plagues South Asian cities. Thus, studying the ecology of urban commensals is important for several reasons. Unlike infrastructure or population density, feeding practices and waste management systems can be modified relatively quickly through regional policy and community engagement—but only if we understand their ecological consequences across the spectral case of coexistence with urban-adapted species (Luniak, 2004; Santini et al., 2019). ***First***, comparative quantitative assessment of their population dynamics, conflict profiles, and management efficacy remains scarce (Ganguly et al., 2018; Priston & McLennan, 2013). Such human-animal relationships extend an opportunity to naturally observe guild formation in nature (Dickman, 2010; Franklin, 1999; Sueur & Huffman, 2024). ***Second***, behavioural heterogeneity within and across populations of the same species warrants integrated, systemic frameworks for understanding and managing coexistence (Beckmann & Berger, 2003; Gordo et al., 2021; Jones & Thomas, 1999). ***Third***, the interconnections between human and animal wellbeing, disease ecology, and social justice have been inadequately synthesised, limiting our ability to develop management strategies that address the multifaceted dimensions of the coexistence crisis (Dhee et al., 2019; Hassell et al., 2017). ***Fourth***, the distinctive role of cultural feeding practices and waste systems in shaping urban animal ecology remains largely unstudied (Kumar et al., 2019c), despite representing tractable intervention points for policy and community engagement. ***Finally***, the intersection of urban (social) conglomerates and a pervasive homogeneity in inadequate solid waste management systems operates at scale. The current lack of their rigorous documentation fundamentally constrains the success of management initiatives and the mitigation of both inter-species conflicts and zoonotic disease transmission. (Kumar et al., 2014, 2018a; 2019a,b).

3. Study design and methods

We adopted a comparative multispecies framework to investigate how the spatial organisation of anthropogenic food subsidies structures coexistence in a tropical megacity. Rather than treating FRDs, rhesus macaques and black kites as independent case studies, we considered them complementary expressions of a common social-ecological process operating across different spatial and temporal scales. The three taxa represent contrasting modes of exploiting human-derived resources: dogs access dispersed subsidies distributed throughout neighbourhoods, rhesus macaques exploit concentrated resource patches associated with religious and institutional settings, whereas kites respond to landscape-scale refuse accumulations and temporally pulsed ritual provisioning. This comparative design enabled us to examine how differences in subsidy distribution, predictability and accessibility shape patterns of multispecies coexistence (details in Gupta & Kumar, 2024; Supplementary material **S.1.2**).

Since the three taxa differ fundamentally in mobility, behaviour and ecology, identical sampling protocols were neither feasible nor desirable. Instead, each dataset was designed to quantify the ecological mechanism most relevant to that system while remaining analytically integrated through the common framework of subsidy-mediated coexistence. FRDs constituted the principal quantitative dataset we present, providing estimates of population density, social organisation and available anthropogenic food subsidies across urban gradients. A natural management intervention involving rhesus macaque translocation at Dr B. R. Ambedkar University, Delhi (AUD), enabled evaluation of recolonisation dynamics under concentrated anthropogenic provisioning. The long-term monitoring of kites documented responses to persistent ritual feeding and refuse-based subsidies across Delhi. These ecological datasets were interpreted alongside ethnographic observations describing how different stakeholder groups experienced, shaped and responded to coexistence (Gupta and Kumar, 2024).

Fieldwork

This study forms part of a long-term research programme initiated in 2012 to investigate the ecology and ethno-zoology of urban commensal scavengers in Delhi (details in Kumar et al., 2019b). Fieldwork combined systematic ecological surveys with long-term ethnographic observations across socioeconomically and culturally heterogeneous neighbourhoods representing the characteristic urban fabric of tropical South Asian cities. Ecological monitoring was conducted across a stratified-random network of 32 sampling plots encompassing semi-natural habitats, residential neighbourhoods, institutional campuses and all three sanitary landfills within Delhi. This long-term field presence facilitated repeated interactions with residents, waste workers, religious practitioners, institutional staff and other stakeholders, providing the ethnographic context within which we interpreted quantitative ecological observations (methodological details in Gupta & Kumar, 2024).

Within this broader study system, intensive surveys focused on dogs, given the highest degree of relational diversity based on their ground-dwelling status that corresponded with variable distribution of and access to anthropogenic food subsidies. AUD’s macaque translocation gave an opportunity to examine social-ecological responses to a translocation intervention undertaken in 2023–2024, while long-term observations of kites were synthesised along. Detailed descriptions of sampling protocols, study sites and field procedures are provided in Supplementary Material S1.3.

Ethnographic framework

To complement ecological observations, we employed a Delphi-inspired ethnographic approach combining participant observation with semi-structured interviews (Mukherjee et al., 2015). Interviews included residents, security personnel, waste workers, institutional administrators, religious practitioners and other stakeholders whose occupations or daily routines brought them into regular contact with urban commensals. Rather than documenting attitudes towards individual species in isolation, the ethnographic component focused on how anthropogenic food subsidies, cultural practices and urban infrastructure shaped everyday experiences of multispecies coexistence (see Fig. 2 in Gupta & Kumar, 2024). Supplementary material **S.1.5.** has ethnographic details on FRDs and macaques; Gupta & Kumar (2024) detailed on how stories ascribe cultural keystone status to avian scavengers in South Asian cities.

Data analysis

Dog densities were estimated using photographic capture–recapture methods. Relationships between FRD density, territorial organisation and anthropogenic food subsidies were examined using correlation analyses at the sampling-plot level. Where necessary, variables were logarithmically or arcsine square-root transformed to satisfy assumptions of normality. Means are presented ±1 SE, statistical tests are two-tailed, and significance was assessed at $\alpha = 0.05$. Quantitative ecological findings were subsequently interpreted alongside ethnographic observations to identify recurring mechanisms linking subsidy organisation, human practices and patterns of multispecies coexistence.

4. Results

Ecology of multispecies coexistence

Across the three focal taxa, availability and access to anthropogenic food subsidies differed markedly in their spatial organisation and temporal predictability, generating contrasting patterns of persistence, aggregation and (re)colonisation within the human-dominated landscape.

We censused 1484 dog individuals using photographic capture-recapture, within a total of 2.95 km^2 area monitored across 14 sampling units. The mean density of FRDs within the city of Delhi was 530±89 dogs/km^2. This value, when extrapolated over the 1500 km^2 of the National Capital Territory of Delhi, yields an estimated population of 7,95,313 FRDs in the capital (range: 6,61,423 to 9,29,203). The average number of packs was 106±14 /km^2, with an estimated 5±1 dogs per pack. The mean male-to-female sex ratio was slightly skewed, at 1.06±0.06 (Supplementary material S.1.4). Food subsidies' estimated availability to FRDs across these diverse neighbourhoods found, on average, 57±16 garbage accumulation points (refuse piles, landfill sections, or concentrated waste zones) and 218±51 feeding stations (including feeding trays, bowls, platforms, or regularly provisioned locations established by residents) per square kilometre. Wealthier areas with better sanitation infrastructure tended to have fewer garbage points but more feeding points, and vice-versa. Extrapolating from sampling site data to Delhi's total urban area, suggests that FRD populations are maintained by approximately 85,109 garbage points and 327,069 feeding stations. During field surveys, feeding stations were typically attended by 2–4 free-ranging dogs, whereas garbage accumulation points generally supported 7–10 dogs actively scavenging or resting nearby (Fig. 1).

Prior to the intervention at AUD in 2023, 148 ± 6 macaques (based on n = 5 independent counts using a double sampling method) occupied the campus and adjacent areas, utilising institutional buildings, green spaces, and a historic *Hanuman* temple where predictable religious provisioning occurred, including a feeding peak on Tuesdays and Saturdays (auspicious *Hanuman* days) (Fig. 2). In response to escalating human-macaque conflicts, approximately 50 individuals were captured using baited cage traps and translocated in eastern Delhi. Despite this substantial removal, macaque numbers returned to pre-intervention levels within one month, demonstrating rapid recolonisation driven by the campus's position within a broader, saturated macaque habitat matrix.

Since the 1960s, the cumulative breeding density of small Indian (black) kites in Delhi has remained stable at 20 ± 7.9 nests/km^2 (range: 0 to ~200 nests/km^2). Dense, semi-colonial nesting was invariably associated with green areas in the city in proximity to muslim settlements, whose ritual meat tossing formed the majority of the breeders' diet. This longitudinal consistency in breeding density has persisted despite the regional decline of vulture-provided ecosystem services and a substantial increase in per capita solid waste production within the metropolitan area. Black-eared kite numbers at Asia's largest landfill, *Ghazipur*, facilitated by the offal from fish, chicken and livestock slaughter facilities used to be as high as 10,000. At Ghazipur, the total numbers fell to less than 1500 between May-August, after migratory kite flocks returned to their breeding grounds in Central Asia. The other two landfills in Delhi, at *Bhalswa* and *Okhla*, which were not associated with large scale meat processing units did not harbour as many kites, with numbers below 1500 throughout the year. Interviews conducted at landfill sites indicated that black kite populations increased following the functional extinction of vultures, which rendered a predictable food resource accessible to other scavenging species.

Together, these quantitative observations reveal that although all three taxa depend upon anthropogenic subsidies, their ecological responses differ fundamentally, mirroring the spatial footprint of refuse dispersion and its temporal predictability, eliciting co-cultural responses. Responding to these patterns, residential communities in this diverse, metropolitan city evoked corresponding cultural organisation of food in the form of human handouts. To examine how these species persist with the human-dominated landscape, we compare them along key ecological and socio-cultural dimensions that shape their access to anthropogenic food resources and the nature of their interactions with people. Table 1 synthesises these comparative dimensions and provides the conceptual framework through which the subsequent ethnographic findings are interpreted.

Table. 1: Comparative social-ecological characteristics of variable mode of adherence to human niche, based on ecological modes (ground-dwelling, arboreal and aerial) of resource exploitation by commensal species in Delhi.

Analytical Axis	Ground-dwelling Commensals (Free-Ranging Dogs)	Arboreal Exploiters (Rhesus Macaques)	Aerial Opportunists (Black Kites)
Spatial Footprint	**Pervasive & Continuous:** Occupy the entire streetscape matrix. Tied to highly distributed waste and neighborhood-level feeding.	**Localized & Bound:** Spatially restricted by architectural features (ledges, roofs) and distinct religious/cultural nodes (e.g. temples).	**Point-Source & Focused:** Highly mobile across macro-scales but forage at specific point-source patches (landfills, ritual meat-tossing points at mosques).
Temporal Dynamic	**Constant & Intergenerational:** Continuous day-and-night cohabitation within human residential boundaries.	**Pulsed & Episodic:** Synchronized with specific worship cycles (e.g., Tuesday/Saturday ritual feeding spikes).	**Pulsed, episodic & Seasonal:** Synchronized with diurnal religious schedules (resident spp.) and seasonal migratory influxes of black-eared kites.
Co-Cultural Architecture	**Individualized & Dyadic:** Based on hyper-local, person-to-animal relationships of care, forming a pervasive informal infrastructure.	**Group-Level & Abstract:** Mediated by broad, religion-mandated tolerance toward the species as a collective spiritual symbol.	**Population-Level & Detached:** Mediated by abstract spiritual obligations to feed scavengers, devoid of individual animal recognition.
Information Resolvability and ensuing conflict mitigation: parsing information landscapes to execute decisions	High density leads to frequent cross-species friction; conflict triggers reactionary spatial exclusion (e.g., Supreme Court culling/removal decrees).	Intricate reading of human routes/escapes; removal fails because the spatial-architectural memory remains intact, prompting quick recolonisation	Read human movements in streets; conflicts manifest as offspring defense or macro-scale systemic hazards (e.g., aviation safety).

Human ecology of multispecies coexistence

The ecological responses to the human niche we reported are inextricably linked with cultural geography. Herein, various facets of human ecology characterise the resources identified and exploited by nonhumans, and how these relate to people who acknowledge ecosystem services, which regulates folk perceptions. The latter encompass both tangible and intangible dimensions, an aspect currently undergoing profound socio-cultural transformation in tropical urbanism. Since urban areas in South Asia invariably face solid waste issues, whose disposal relies on informal human labour and animal scavenging, the relations aspects, based on highly distinct encounter patterns, vary across stakeholders. Below, we summarise the core aspects from long term ethnographic research and the targeted semi-structured interviews from 2023-2026. The interview and ethnographic details are accessible in Supplementary material S.1.5.

(i) Recognition, familiarity and socio-cultural mediation

Relationships with ground-dwelling commensals were highly individualised. Residents who regularly provision neighbourhood commensals reported reciprocal recognition, with dogs responding to familiar people through visual cues, vocalisations and daily routines. This familiarity created differentiated geographies within the same streetscape, where feeders perceived dogs as companions whereas transient workers, waste collectors and delivery personnel frequently interpreted the same set of animals as unpredictable or aggressive. In contrast, relationships with rhesus macaques were largely group-mediated. Human–macaque interactions primarily occurred within shared institutional environments and religious locales, where patterns of tolerance characterised predictable human–animal relations sustained by ritual provisioning. Conversely, conflicts were typically linked to macaque troops raiding non-religious sites, which occurred with higher frequency on Mondays, Wednesdays, Fridays, and Sundays. On Tuesdays and Saturdays, macaque aggregations shifted toward temples, coinciding with auspicious days dedicated to the deity *Hanuman*. Black kites represented an even more abstract level of interaction. Ritual meat provisioning and refuse disposal supported large aerial aggregations. Due to overlapping ecological niche and similarity in plumage, people misidentified kites as vultures. These observations reveal a continuum from individual-level recognition to population-level cultural associations, based on variable adherence to human niche.

Fig. 1. Spatial and temporal dimensions of human-dog coexistence in Delhi. ***(Left)*** Free-ranging dogs provisioned near shops chase a scooter rider, demonstrating territorial aggression in feeding-concentrated zones. ***(Center)*** A homeless person and street dog share pavement space, illustrating intimate cohabitation. ***(Right)*** Free-ranging dogs occupy road corridors during night hours when human/vehicular traffic subsides, creating navigation hazards for nocturnal commuters. These scenes reveal how coexistence is negotiated across spatial (commercial areas, pavements, roads), temporal (day/night), and socioeconomic gradients—demonstrating that human-dog

relationships are dynamic, context-dependent interactions rather than fixed arrangements. Photos: Thinkpaws field research, Delhi 2023-2024.

(ii) Occupational exposure and differential vulnerability

Conflict risk was strongly arranged by infrastructure, occupation and everyday movement. Individuals whose livelihoods required prolonged exposure to public space—including security guards, waste workers, street vendors and delivery personnel—reported substantially greater interactions with urban commensals than residents occupying enclosed buildings or private transport. At AUD, security personnel consistently described being targeted by macaques while occupying narrow entrances and isolated guard posts, whereas faculty members generally avoided encounters by remaining indoors or modifying movement schedules. Similar patterns emerged for dogs, where older adults and blue-collar workers altered travel routes or carried sticks in response to perceived aggression. For aerial scavengers, vulnerability was expressed at larger spatial scales, with airport personnel near landfills described enormous flocking as a nuisance and safety concerns. For the resident breeding kites, the conflict caused during offspring defense was wonderfully tolerated, since people acknowledged that it only for a short, two month breeding period. Across all three taxa, conflict was therefore mediated less by species identity than by unequal exposure to shared urban spaces (Fig. 2 &3).

Fig. 2. Macaque foraging strategies and conflict contexts at Dr B R Ambedkar University Delhi. Rhesus macaques exploit dual food sources: direct human provisioning (center-left) and waste accumulation (center-right), with refuse providing persistent foraging opportunities reflecting inadequate sanitation infrastructure. Individuals forage on paved surfaces and building perimeters (left, right), demonstrating habituation to institutional architecture and high human-traffic zones. This resource predictability and architectural accessibility embolden macaques toward close human proximity, generating conflict scenarios particularly affecting spatially constrained outdoor workers. Photos: AUD campus, 2023-2024.

(iii) Spatial memory and the limits of reactive interventions

Ethnographic evidence consistently indicated that management interventions produced only temporary changes when the underlying resource landscape remained intact. Following macaque translocation, respondents described an initial reduction in encounters that disappeared within weeks as neighbouring troops recolonised resource-rich institutional campuses. Likewise, residents questioned whether dog sterilisation programmes altered everyday interactions, arguing that food provisioning, waste accumulation and neighbourhood familiarity continued to shape local coexistence irrespective of demographic intervention. This also varied across regions, since sterilisation initiatives focused on posh localities, frequently overlooking the conflicts within middle and lower class settlements where solid waste issues are more pronounced. Long-term observations of black kites similarly demonstrated persistent use of ritual feeding sites and waste infrastructure despite broader environmental change. Since the migratory and non-breeding birds are a substantial part of kite populations in these long-lived species, regional extinction of experience with scavenging ecosystem services could alter the future course of coexistence. Together, these findings suggest that animals respond to enduring spatial memories and predictable anthropogenic subsidies rather than to short-term management actions alone.

(iv) Ecological memory and multispecies governance

Interviews also revealed that coexistence was shaped by historical ecological relationships extending beyond the focal species themselves. Administrative staff at AUD recalled the former use of Hanuman langurs *Semnopithecus entellus* as biological deterrents for macaques, followed by their replacement with human "monkey chasers" after legislative restrictions prohibited captive langur use in 2012. In August-September 2023, the municipality installed life size langur cutouts to keep macaques at bay near buildings that hosted G20 meetings: it failed, since macaques got habituated. Respondents interpreted this transition as evidence that contemporary management increasingly attempts to imitate ecological processes that once occurred naturally (Fig. 3). Similar narratives emerged around feeding practices for dogs, macaques and kites, where ritual provisioning persisted despite growing public-health concerns, reflecting the coexistence of ecological, ethical and religious motivations. Collectively, these ethnographic accounts demonstrate that multispecies coexistence in Delhi is embedded within long-term cultural memory and changing governance, rather than being reducible to contemporary conflict alone.

Fig. 3. From sympatric competition to failed mimicry: The evolution of macaque management in Delhi. ***(Left)*** Common langur chasing rhesus macaque, illustrating natural interspecific competition that historically coexisted with macaque populations. Prior to 2012, institutions employed captive langurs as biological deterrents. ***(Right)*** Following ethical prohibition of langur use (PETA intervention, 2012), Municipal Corporation of Delhi introduced "monkey chasers"—trained workers imitating langur calls and appearance while pursuing macaques.

This substitution fails because macaques distinguish genuine threats from human mimicry, quickly habituating to artificial deterrents. Delhi's regional langur extinction severed the ecological relationship management now attempts to replicate symbolically, demonstrating that effective coexistence requires actual ecological processes, not superficial imitation. *Photos: representative sympatric interaction; and MCD monkey chaser generated by Gemini NanoBanana, Delhi 2023.*

5. Discussion

5.1 Human subsidies, culture and infrastructure organise multispecies coexistence

a) Human subsidies create distinct multispecies architectures of tropical cities

Our findings demonstrate that multispecies coexistence in tropical cities is not simply determined/sustained by the distribution or abundance of urban-adapted animals. Rather anthropogenic resources organised across space, time and culture sustain these ecosystems. Although FRDs, macaques and kites differ fundamentally in locomotion, social organisation and habitat use, they converged upon a common ecological dependence on predictable human-derived subsidies—a tropical urbanism convention (Fall & Jackson, 2002; Fehlmann et al., 2021a). The quantitative and ethnographic components of this study jointly indicate that the architecture of these subsidies are variably dispersed and are further changing in response to urban infrastructure, e.g., FRDs' growing reliance on roads as primary territories/conduits (Amin, 2013; Angel et al., 2011; Barua, 2023; Bobiec et al., 2021; Dupont & Gowda, 2020; Hinchliffe et al., 2005; Lim & Sodhi, 2004; Narayanan, 2017; Philo, 1995). Animals responded to the spatial distribution, temporal predictability and accessibility of food resources, while human communities simultaneously negotiated these interactions through cultural practices, drawing folk biological inspiration based on occupational routines and institutional responses: it involved both tangible and intangible aspects (Derham & Mathews, 2020; Dhee et al., 2019).

This comparative perspective shifts the focus from conflict resolution as cases of species-specific interventions; it warrants broader comprehension of processes through which urban ecosystems are co-produced through human-animal co-cultural entanglements (Sueur & Huffman, 2024). Dogs, macaques, kites, etc. should therefore not be viewed as independent case studies, but as complementary expressions of a common social-ecological phenomenon. Together, urban fauna illustrate how variable modes of exploiting the human niche generate distinct movement ecology, aggregation, recognition and conflicts. Rather than asking why individual species become urban "problems" (Allen et al., 2023; Reese, 2005; Srinivasan, 2013), our results suggest a more fundamental question: *how does variable availability and access to anthropogenic subsidies generate distinct relational architectures between people and urban wildlife*?

This distinction has important implications for understanding tropical urbanism. Urban ecological research has frequently quantified animal abundance while treating food resources as a relatively homogeneous component of the landscape. Our results instead demonstrate that the ecological consequences of anthropogenic subsidies depend upon their organisation. Distributed neighbourhood feeding created markedly different ecological relationships from concentrated religious provisioning or large-scale waste accumulation. Consequently, similar quantities of food generated very different ecological outcomes depending upon how those resources were encountered by animals operating in ground-dwelling, arboreal or aerial environments.

b) Spatial organisation of anthropogenic subsidies structures coexistence

The three focal taxa occupied different regions of a common subsidy landscape. FRDs exploits resulted in relatively continuous territorial occupation alongside humans (Gompper & Gompper, 2013). Macaques concentrated around discrete institutional campuses and religious sites where predictable provisioning and suitable architectural refuges (e.g. medieval and colonial-era architecture) occurred together. It produced predictable, localised conflict hotspots (Baviskar, 2020; Ganguly et al., 2018; Gupta, 1981). Black kites responded to resource concentrations operating at still larger spatial scales, including landfills, slaughterhouse waste and ritual meat provisioning, generating dense aerial aggregations around predictable feeding landscapes (Kumar et al., 2025).

The principal difference in commensal ecology lies in the geometry of resource accessibility, contingent on familiarisation with the information landscape (McComb et al., 2001). Dogs could tolerate familiar people/animals, and, in turn be tolerated as encountered near subsidies throughout the street network. Domestication has enabled repeated familiarisation with residents, based on coat colours (Larson et al., 2013). This often led to relatively stable territorial boundaries. Macaques accessed concentrated food sources linked to campuses, navigating three-dimensional urban architecture. They chose fixed points and cycles of aggregation. Black kites integrated information, both at landscape and micro-scale, ensuring nesting/roosting in proximity to accessible resource patches. Their cross-scalar information parsing supported ecological stability despite substantial environmental change (N. Kumar et al., 2018; McComb et al., 2001; Nagendra et al., 2014; Paul & Nagendra, 2015).

The stability of black kite breeding densities over more than half a century provides an instructive comparison. Despite the regional disappearance of vultures, dramatic urban expansion and increasing waste generation, breeding densities remained remarkably constant. Likely because the cultural and infrastructural processes limited the other vital resource aspect: nesting substrate, which constrained population-level responses (Jordan et al., 2020; Kumar et al., 2019a). However, kites replaced vultures on Delhi’s landfills (Gupta & Kumar, 2024). Similarly, rapid recolonisation of macaques at AUD, following translocation, reflected the continued presence of predictable religious provisioning and structurally suitable habitat, nullifying targeting individual animals. At neighbourhood scales, dog densities closely tracked anthropogenic feeding infrastructure, indicating that distributed food subsidies influenced both territorial organisation (packs per unit area) and local abundance (overall density variation) (see, e.g., Cavé, 2014; Kumar et al., 2019c; Kumar et al., 2017).

Viewed together, these findings suggest that anthropogenic subsidies and animals it supports should be considered a defining component of tropical urban habitat, not just an artifact (Allen et al., 2017). Feeding platforms, refuse accumulation, religious offerings and waste infrastructure function as ecological features analogous to natural habitat elements, determining where animals establish territories, concentrate activity and repeatedly interact with people. Urban planning has traditionally disregarded these. Such features have repeatedly been considered as disparate matters of sanitation, religious practice or municipal governance (Dupont & Gowda, 2020; Gowda, 2021; Gupta & Gupta, 2017). Our results indicate that they simultaneously constitute ecological infrastructure supporting multispecies communities.

c) Co-cultural architecture links ecological and social processes

The ecological patterns documented here cannot be understood independently of the cultural practices through which resources become available; unfortunately, it includes poor waste disposal infrastructure. Across Delhi, anthropogenic subsidies reflected deeply embedded social behaviours rather than accidental food availability. Ritual feeding, household provisioning and informal waste management collectively created predictable opportunities that animals repeatedly exploited. For instance, over the last 25 years, Delhi has seen a simultaneous increase—in tune of 200-300%—to its built-space, people, FRD and vehicular densities, and its per-capita income and solid waste production (Government of India, 2024; Kumar et al., 2017; Livestock Census of India, 2019; Paul & Nagendra, 2015; Shukla, 2025; UNO, 2018). These interactions therefore extend beyond resource ecology into what may be described as co-cultural architecture (Alberti, 2008; Lin et al., 2021; Sueur & Huffman, 2024): the socially organised pathways through which ecological relationships are continually produced and maintained. This co-cultural architecture differed substantially among the three taxa (Jackson et al., 2017; Wilcox et al., 2021). Human responses corresponded to occupational responsibilities, architectural designs, and collective utilization patterns, as individuals mapped multispecies encounters within their daily routines, exhibiting affiliation, aversion, or widespread indifference (Braczkowski et al., 2023; John et al., 2021; Thangaraj et al., 2025). This progression from individual to collective relationships represents one of the principal comparative insights emerging from the study. The degree to which coexistence depended upon individual recognition declined as spatial scale increased (Govindrajan, 2015).

Our ethnographic assessments demonstrated relationships are neither uniformly positive or antagonistic. Communities frequently expressed simultaneous appreciation and concern regarding the same species. Dogs were regarded as companions, protectors and recipients of patronising moral obligation. Simultaneously, they were also associated with bite risk and territorial aggression. Religious provisioning of macaques persisted despite widespread recognition that predictable feeding contributed to conflict (Ganguly et al., 2018). Black kites were simultaneously valued as scavengers and regarded as aviation hazards when large aggregations developed near critical infrastructure like airfields. Such apparent contradictions are not inconsistencies but inherent properties of coexistence in densely populated tropical cities, where ecological, cultural and ethical considerations continuously overlap (Kumar et al. 2019c).

Rather than viewing cultural practices simply as drivers of conflict, our findings suggest that they constitute ecological processes in their own right. Religious traditions, feeding customs and waste disposal routines influence resource predictability in much the same way that seasonal productivity shapes wildlife populations in natural ecosystems. Animals responded to these predictable cultural rhythms through behavioural adjustment, spatial memory and learned movement patterns. Ecological and cultural processes thus became inseparable components of the same urban system (Broekhuis et al., 2021; Holt, 2008; Sueur & Huffman, 2024).

d) Information resolvability as a mechanism of coexistence

Beyond resource distribution, the comparative analysis points towards a second mechanism underlying coexistence: the ability of humans and animals to develop predictable mutual expectations. We propose that successful coexistence depends partly upon information resolvability—that is, the extent to which animals and people can reliably interpret recurring features of their shared environment.

Regular feeders described reciprocal recognition developed through repeated daily encounters, whereas unfamiliar pedestrians frequently experienced the same territories as unpredictable and potentially threatening. Conflict therefore depended not solely upon dog density but upon the degree to which both parties could anticipate mutual behaviours. Similarly, residents altered movement schedules, selected alternative routes or adopted defensive strategies in response to previous encounters, demonstrating that humans continually updated behavioural expectations in parallel with the animals themselves (Albuquerque et al., 2016; Benítez et al., 2022).

Comparable processes emerged in the macaque system. Security personnel repeatedly occupying constrained outdoor locations experienced substantially greater conflict than faculty members working primarily indoors (see Kumar et al., 2018a, b; Gupta & Kumar, 2024). This difference reflected not only exposure but repeated interactions occurring within highly predictable spatial settings (e.g., Kumar et al. 2018b; 2019b). Following translocation, recolonising macaques entered landscapes where previous behavioural expectations between humans and animals had been disrupted. The temporary increase in perceived conflict reported by respondents is therefore consistent with the breakdown and subsequent reconstruction of locally established interactional routines, in addition to merely increasing animal abundance (Francis & Chadwick, 2012; Sciences et al., 2011).

5.2 Human geography configures multispecies coexistence

a) Reactive management targets animal displacements, overlooking coexistence contours

Management interventions had the fault line in targeting animal populations, a consistent pattern across all three systems. Agencies/people overlook the social-ecological nature of these ecosystems. Consequently, interventions that led to initially visible conflict reduction trends seldom sustain (Anderies et al., 2007; Doebeli et al., 2021; Ross et al., 1993; Wong & Candolin, 2015).

Macaques troops exhibit highly dynamic socio-ecologies, undergoing fission-fusion processes within 24-hour cycles. Troops, therefore have overlapping territorial boundaries, which led to quick recolonisation of AUD campus during September-October 2023 (Cunha Silva et al., 2025; Evans & Gawlik, 2020; Ganguly et al., 2018; Oro et al., 2013; Reese, 2005; Tella et al., 2020; West & Jones, 2022). On the other hand, variation in how many dog packs could occur in an area was explained more consistently by the distribution of ritual feeding than by incidental waste alone, indicating distinct axes of neighbourhood resource organisation and its exploitation, which likely entails site-specific behavioural phenotypes. Random removals/translocations, which do not factor such resource specification and behavioural phenotype could affect dogs' well-being (Bhattacharjee et al., 2018, 2018; Bhattacharjee & Bhadra, 2022; Majumder et al., 2014; Majumder et al., 2014).

Taken together, these findings suggest that many urban wildlife interventions are directed at ecological consequences rather than ecological causes (Santini et al., 2019). Removal, deterrence or sterilisation modify animal numbers or behaviour temporarily, whereas resource landscapes that drive these processes remain largely unchanged (Dickman, 2010; Ganguly et al., 2018; Priston & McLennan, 2013). Such interventions therefore become cyclical, requiring repeated implementation that limits longevity of convivial coexistence (Galbreath et al., 2014; Silk et al., 2019).

This distinction is particularly relevant in rapidly urbanising tropical cities where feeding practices, refuse production, informal waste disposal and institutional food subsidies are not exceptional events but recurring components (Dupont & Gowda, 2020; Gowda, 2021; Gupta & Gupta, 2017). Consequently, animals experience these landscapes as predictable ecological systems, offering varied opportunities. Unless management modifies the organisation of these subsidies, interventions will likely yield suboptimal results (Ganguly et al., 2018). However, this does not imply that population management lacks value. Rather, it suggests that demographic interventions should be embedded within broader strategies that recognise how cultural practices, waste infrastructure and urban design jointly influence animal populations (Anonymous, 2023; Dupont & Gowda, 2020; Gowda, 2021). Managing coexistence therefore requires understanding not only animal ecology but also the human behaviours continually reconstructing urban habitat (Bhattacharjee & Bhadra, 2020; Chimento & Farine, 2024; D'Aniello et al., 2018).

b) From species management to relationship management

Perhaps the most important implication of this study is that urban coexistence should be understood primarily as a property of relationships. In case of biotic communities that are relatively unaffected by anthropogenic resources/subsidies, the demographic parameters essentially encompass behavioural processes. Hence, conventional management frequently assumes that reducing animal abundance necessarily reduces conflict. Our comparative analyses suggest that this assumption is often incomplete because conflict emerges through repeated interactions among humans, animals and the environments they jointly configure (Nyhus, 2016; Wong & Candolin, 2015).

The long term ethnography illustrated this relational perspective. Respondents rarely evaluated animals solely according to abundance. Instead, perceptions depended upon familiarity, occupation, cultural values, previous encounters and patterns of daily movement (Gupta & Kumar, 2024). Dogs recognised by neighbourhood feeders were interpreted differently by blue collar workers. Security guards occupying exposed outdoor locations experienced macaques differently from faculty/students working within enclosed buildings (Braczkowski et al., 2023; John et al., 2021; Thangaraj et al., 2025). Black kites were simultaneously perceived as culturally valued scavengers, indicators of environmental change and hazards to aviation depending upon the observer's institutional locus.

These observations suggest that identical animal populations may generate very different coexistence outcomes depending upon the relational contexts through which encounters occur. Consequently, coexistence cannot be reduced to demographic metrics alone. Instead, ecological abundance, cultural meaning and patterns of encounter jointly determine how species are experienced within urban landscapes (see Barua, 2023; Bhalla et al., 2021; Hinchliffe & Whatmore, 2006). This perspective also helps explain why conflicts frequently polarised communities. Different stakeholder groups occupy distinct social-ecological positions within the same city (Barua, 2023; Doron, 2021), e.g., ritual feeding may be an act of compassion but generates conflict risks for others. These contrasting experiences arise not because one interpretation is correct and another incorrect, but because coexistence itself is socially heterogeneous (Almada, 2011; Baker et al., 2014; Beumer & Martens, 2015; Cavé, 2014).

Recognising this heterogeneity shifts urban wildlife governance from managing species towards managing relationships. Rather than simply asking how many, or which animals/taxa should be present, management increasingly needs to consider encounter patterns: *which stakeholder (including nonhumans) experience consequences, how spatio-temporally predictable they are, and how urban infrastructure shapes opportunities for positive or negative interactions*. Such questions naturally integrate ecology with environmental justice, urban planning and public health rather than treating these disciplines as independent domains (Amin, 2013; Angel et al., 2011; Barua, 2014; Bradley & Altizer, 2007).

c) Towards predictive, culturally informed tropical urban ecology

Although this study is situated within Delhi, its broader contribution lies in proposing a comparative framework for understanding coexistence across rapidly urbanising regions of the Global South. Tropical cities frequently combine rapid infrastructural expansion with strong cultural traditions of coexistence, informal waste economies and dense multispecies communities. These conditions generate urban ecosystems fundamentally different from those on which much contemporary urban ecology has been based (Angeoletto et al., 2025; Kumar et al., 2025).

Our comparative approach suggests four interacting dimensions that may prove useful for understanding these systems. ***First***, the spatial footprint of anthropogenic subsidies determines how animals distribute themselves across cities. ***Second***, temporal rhythms of human activity create predictable resource pulses that structure animal movement and behaviour. ***Third***, co-cultural architecture links ecological processes to religious practices, institutions and everyday social organisation. ***Finally***, information resolvability influences whether repeated encounters generate familiarity, tolerance or conflict.

These dimensions operate simultaneously across taxa despite considerable biological differences. Dogs, macaques and black kites therefore illustrate not independent ecological stories but different positions along a common continuum of human dependence. Correspondingly, conflict transitions from neighbourhood territoriality to institutional aggregation and finally to landscape-scale management challenges. This continuum provides a unified framework for comparing urban commensals that would otherwise appear ecologically unrelated (e.g., Carricondo-Sanchez et al., 2019). This framework is predictive: knowing how anthropogenic subsidies are organised within cities should allow anticipation of where different forms of coexistence are likely to emerge. Future work can test these predictions across additional taxa including pigs, cattle, crows, pigeons and rodents, evaluating the broader applicability of subsidy-mediated coexistence across tropical urban ecosystems (Fehlmann et al., 2021b; Hunold & Mazuchowski, 2020; Nyhus, 2016).

5.3. Limitations and future directions

Our analyses represent different forms of evidence. Despite the limitation over constituting identical datasets, these systems were deliberately integrated because each illuminated complementary aspects of subsidy-mediated coexistence. Future comparative studies employing equivalent quantitative approaches across multiple taxa would provide opportunities to evaluate the generality of the framework proposed here. Similarly, although our ethnographic findings consistently converge with ecological observations, future work should investigate how information landscapes shared between people and animals are co-developed through repeated encounters and how changes in urban infrastructure alter these processes through time (DDA, 2017; Dupont & Gowda, 2020). Longitudinal studies combining behavioural/population ecology, social science and spatial analysis would substantially strengthen predictive understanding of coexistence dynamics.

5.4. Conclusions

This study demonstrated that apparently disparate coexistence outcomes can be understood through a common social-ecological framework, which substructures human-animal coexistence in a tropical megacity. Across ground-dwelling, arboreal and aerial systems, anthropogenic subsidies structured ecological opportunity, while cultural practices, urban architecture and repeated encounters mediated how these opportunities were realised. The resulting co-cultural patterns likely differ within and across cities, limiting straight-jacket urban wildlife management because the organisation of human-derived resources vary, not because the underlying ecological processes were fundamentally distinct. This perspective reframes coexistence as a dynamic property emerging from reciprocal interactions between people and animals inhabiting shared urban landscapes.

Cities should therefore be viewed not merely as environments occupied by wildlife but as continuously negotiated ecosystems in which ecological processes, cultural practices and infrastructure jointly shape shared lives of human and non-human residents. Returning to the question posed at the outset of this paper, the future of tropical urban coexistence is unlikely to depend upon whether cities contain more or fewer dogs, macaques or kites, etc. Rather, it will depend upon how societies organise the food systems, built environments and cultural practices through which relationships with these species are continually reconstituted (i.e. co-cultured). Recognising this shift—from managing populations to understanding and shaping the architecture of coexistence—offers a pathway towards more predictive, equitable and ecologically informed urban futures.

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Author Contributions

NK conceived the study, designed the comparative framework, conducted long-term kite/macaque/ethnographic research, analysed and interpreted the data, and wrote the manuscript. BS conducted the majority of free-ranging dog field surveys, assisted with dog identification and territory mapping, and contributed to verification of dog population and resource-subsidy data. Both authors reviewed and approved the final manuscript.

Ethical Statement

The ethical approval for dog study was via permit number 2023/ER/Canine Conundrums/01, from Thinkpaws, with validity: 29.04.2023 to 31.12.2027 and the M.Sc. dissertation committee of Chaudhary Charan Singh University, Meerut, Uttar Pradesh. Since this study was non-invasive and free-ranging dogs are not under the Wildlife Protection Act, no specific permission from the Department of Forest and Wildlife, Government of NCT of Delhi was required.

Declaration of AI use

This article's sections were revised for grammatical mistakes and were provided rewording and sentence restructuring suggestions. The software tool 'Grammarly' (App version 1.2.155.1657, embedded in the Google Doc.) was used between 27.11.2025 and 29.06.2026. In addition, Figure 3 was created in Gemini NanoBanana.

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Supplementary Material SI

Cultural practices and food subsidies shape the architecture of multispecies coexistence in a tropical megacity

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Supplementary Material S1

S1.1. Background

a) Ground-dwelling commensals: Dogs (*Canis lupus familiaris*), arguably the first domesticated species, are the most widespread carnivores globally, with populations estimated at approximately one billion individuals. In urban contexts, ecologists classify dogs into overlapping categories—pet, street, free-ranging, and feral—based on their behavioural relationships with humans and their dependence on human provisioning (Vanak & Gompper, 2009). Approximately 80% of dogs worldwide remain free-ranging, exhibiting varying levels of adherence to the human niche and displaying diverse interdependencies with urban communities.

The scale of the challenge is staggering. The Indian subcontinent harbours the majority of the world's free-ranging dogs (Vanak, 2017), yet we have not explored relational patterns between human densities, dog densities, and conflict ecology. In tropical cities like Delhi, free-ranging dog (FRD) populations create a complex mosaic of social and breeding units that operate across human settlements, generating multilayered challenges: conflict with vulnerable human populations (children, elderly, waste workers), disease transmission risks (particularly rabies), and ethical dilemmas regarding population management (Sharma, 2023). Current estimates suggest 20 million annual dog bites globally—one every two seconds—with India experiencing approximately 40% of global rabies deaths. These conflicts exact substantial costs: 40 million human working days in recovery and £21 million in prophylactic treatment annually across India alone (Vanak, 2017). Critically, these figures capture only bite incidents, excluding the broader spectrum of disturbances—barking and chasing behaviours, livestock conflicts and losses, and inter-species tensions with other urban commensals and wildlife (Gompper & Gompper, 2013). This data gap extends beyond incidence reporting: we poorly understand how anthropogenic food subsidies translate into dogs' numerical responses (abundance and distribution) across different urban contexts.

Traditional interventions—culling, mass sterilisation, or translocation—have generated cycles of retaliation and counter-protection, creating what researchers term the "intervention paradox," wherein management solutions escalate rather than resolve underlying tensions. The behavioural heterogeneity within FRD populations, coupled with their capacity for rapid learning and adaptation to urban niches, demands quantitative assessment of population dynamics, conflict patterns, and the efficacy of evidence-based management strategies. Delhi's recent experience with dog management interventions illustrates how underestimating rapid recolonisation potential contributes to management failure (India Legal, 2022; Reporter, 2021; Shukla, 2025).

b) Arboreal urban exploiters: Rhesus macaques (*Macaca mulatta*) exemplify a fundamentally different mode of urban adaptation compared to ground-dwelling commensals. Unlike dogs, macaques do not generally form dyadic bonds with humans but instead exploit urban resources—particularly refuse and ritually provisioned foods—through their three-dimensional mobility. This arboreal advantage enables them to raid human settlements and retreat to trees, woodlots, or rocky/building outcrops beyond human reach, rendering traditional ground-based management ineffective. Their opportunistic intelligence, combined with rapid learning and cultural transmission within social groups, allows macaque troops to identify and exploit new resource patches.

We lack comprehensive knowledge of how arboreal species like macaques respond to urban food sources and territorial pressures. Urban infrastructure development, increasing waste generation, and shifting cultural norms regarding wildlife tolerance occur against a backdrop of macaque behavioural profiles, sentient of these changes. Yet these complexities remain poorly understood and inadequately addressed by traditional management approaches (Barua et al., 2013; Braczkowski et al., 2023; Dickman, 2010; Nyhus, 2016; Torres et al., 2018). Interventions documented across Delhi and other megacities—removal of problematic individuals or entire troops—have shown limited long-term success and often generate unintended consequences, including establishment of new problem troops in neighbouring areas. Cases of rhesus macaques exemplify how ritual feeding and high human footfall contributed to macaque territorial instability, making conflict resolution through displacement ineffective (Deol, 2023; Govindrajan, 2015; Rittem et al., 2024). A critical gap exists in quantitative understanding of macaque population dynamics in urban settings, conflict escalation pathways, and the spatial and temporal factors that determine management outcomes. Such understanding is essential for developing targeted, evidence-based interventions that balance conservation concerns with legitimate human safety and welfare priorities (Ganguly et al., 2018; Priston & McLennan, 2013; Radhakrishna et al., 2012; Ross et al., 1993; Wu et al., n.d.).

c) Aerial opportunists: Black kites (*Milvus migrans*), studied through long-term research in Delhi by Gupta & Kumar (2024), exemplify how aerial scavengers navigate complex urban landscapes while generating novel forms of human-animal conflict (Kumar, Jhala, et al., 2019). Unlike terrestrial or arboreal species, aerial commensals present distinct challenges including aviation safety hazards when large congregations (Kumar et al., 2020) create airspace conflicts (Arrondo et al., 2021; Baxter et al., 2003; Sodhi, 2002). The seasonal influx of migratory black-eared kites (*Milvus migrans lineatus*) generates massive communal foraging roosts in and around landfills, with aggregations numbering in the thousands at single sites (Kumar et al., 2020).

Recent studies have identified how avian scavengers adjust their foraging and nesting behaviours in response to human activity patterns and cultural beliefs (Gupta & Kumar, 2024; Kumar et al., 2018a; 2019a,b). These large avian assemblages create significant nuisance issues for surrounding communities—including noise, waste dispersal, and nesting conflicts—while simultaneously raising largely unexplored concerns about disease transmission (particularly through scavenging of diseased animal carcasses) and toxicant bioaccumulation in urban food webs (Kumar et al., 2019c; Xu et al., 2016). Researchers have largely overlooked the ecological impacts of waste-based biomass availability, despite cursory evidence showing significant effects on urban-adapted birds and mammals at garbage points and landfills (Katlam et al., 2018). The role of aerial scavengers in maintaining ecosystem services (carrion removal, nutrient cycling) versus their ecological and health liabilities remains inadequately quantified, particularly in tropical urban contexts where sanitation infrastructure and wildlife management intersect.

S1.2. Study system

Delhi as a multispecies urban landscape

Delhi is seated within a network of rapidly expanding megacities, is home to ~35 million people and spans an area of 1,500 km2 (Census India 2011, UNO 2018). The national capital attracts people from all over the country for livelihood. The city's layout is polycentric and diverse, featuring a variety of urban configurations that defy a linear urban-rural gradient, emblematic of South Asian urbanism (Shahmoradi 2013). Delhi displays three critical aspects that likely influence the interactions between humans and urban commensals. ***First***, inadequate solid waste disposal systems have led to the emergence of informal livelihoods, which are central to waste processing and contribute to the persistence of roadside garbage piles (see Kumar et al. 2019c for details). These piles vary in size and content, fostering close interactions among the urban poor, various facultative/obligate scavengers (such as kites,dogs, macaques, crows, egrets, and pigeons), and opportunistic mammals like stray dogs, rats, and cattle (Figure 1). The presence of this detritus and associated non-human organisms imparts a distinctive visual and olfactory ambiance to tropical urban settings like Delhi (Gupta and Gupta 2017), epitomizing the sensory aspects of tropical urbanization (Doron 2021). ***Second***, increasing meat consumption in and around Delhi is creating subsystems of animal waste. These changes are leading to increasing volumes of unsegregated waste and animal byproducts, and a scarcity of suitable waste disposal sites. ***Third***, conflicts have arisen among various civic authorities tasked with waste management, leading to an increase in negative perception and low tolerance about certain animal scavengers (Kumar et al. 2019c).

S1.3. Ecological sampling

Free-ranging dog surveys

Because large areas of Delhi comprise inaccessible private properties and free-ranging dogs attain exceptionally high densities, continuous sampling across the entire city was impractical. We therefore employed a stratified sampling design consisting of 14 intensive survey plots selected randomly from the original network of 32 long-term monitoring plots (Kumar et al., 2019b). Individual plots averaged approximately 0.2 km² of contiguous accessible habitat and collectively represented the range of residential, commercial and semi-natural environments present across Delhi. The selection of sampling plot size was contingent upon the largest FRD pack area in Delhi, which closely corresponded to the dimensions of municipal waste management in respective residential blocks. However, a standardised shape or a standardised surface of 0.2 km^2 could not be attained for all plots because of constraints. The dimensions of each plot were determined by the typical territory size of neighbourhood dog packs and the spatial organisation of municipal waste infrastructure. Plot geometry varied where access was constrained by private property, although adjacent inaccessible areas possessed comparable urban characteristics and were not expected to bias density estimates. Territories intersecting plot boundaries were repeatedly surveyed to minimise edge effects during density estimation.

Repeated surveys were conducted between April and August 2023. Observers systematically searched roads, parks, open spaces, buildings, vehicles and other refuges used by free-ranging dogs. Occasional dog-bark playbacks were employed to detect individuals hiding under cars, etc. Individual packs were identified through repeated observations of territory occupancy and photographic capture–recapture methods. Territories were revisited at approximately eight-day intervals, during which the spatial distribution of anthropogenic food subsidies—including garbage accumulation points and regularly provisioned feeding stations—was quantified. Dog density was expressed as individuals and territorial packs per square kilometre. Additional observations of diel activity budgets were conducted to characterise temporal variation in habitat use.

Macaque study system

Dr B. R. Ambedkar University is situated within the historically macaque-dominated landscape surrounding Kashmere Gate and Old Delhi Railway Station. This urban matrix comprises long-established markets, institutional buildings, medieval architecture, religious sites and green spaces that have supported rhesus macaque populations for decades. During 2023–2024, approximately fifty macaques were translocated from the campus following escalating human-animal conflict. Subsequent field observations documented recolonisation dynamics and associated stakeholder experiences.

Black kite monitoring

Long-term monitoring of black kite breeding populations, landfill aggregations and ritual feeding sites formed part of the broader Delhi scavenger research programme initiated in 2012. Detailed sampling methods have been published previously (Kumar et al., 2014; Kumar et al., 2018; Kumar et al., 2019) and are therefore not repeated here.

S.1.4. Summary of quantitative estimates

Table 1: Free-ranging dog population characteristics and anthropogenic resource availability across 14 sampling sites in Delhi, India (April-August 2023). The limited size of Site 5 is attributed to the entire area of the top of *Ghazipur* landfill.

Site ID	Sampled Area (km^2)	Photo captured dogs	# of packs	Mean pack size	Density (dogs/km^2)	Pack density (packs/km^2)	Sex Ratio Adult (♂ : ♀)	#Feeding trays/km^2	#Garbage heaps/km^2
1 (Central)	0.38	335	59	5.68	881.58	155.20	1.05	552.63	10.53
2 (Central)	0.43	177	44	4.02	411.63	102.30	0.86	300.00	4.65
3 (Central)	0.28	174	46	3.78	621.43	164.20	0.85	410.71	28.57
4 (East)	0.20	56	6	9.33	280.00	30.00	1.16	15.00	25.00
5 (East	0.05	70	6	11.67	1400.00	120.00	1.00	0.00	400.00
6 (East)	0.14	85	12	7.08	607.14	85.70	1.30	0.00	142.86
7 (West)	0.20	56	20	2.80	280.00	100.00	1.25	350.00	20.00
8 (North)	0.17	119	32	3.72	700.00	188.20	0.99	429.41	5.88
9 (North)	0.19	23	4	5.75	121.05	21.05	1.10	284.21	21.05
10 (Northwest)	0.19	18	4	4.50	94.74	21.05	1.59	42.11	31.58
11 (Northwest)	0.16	66	16	4.13	412.50	100.00	0.83	25.00	18.75
12 (South)	0.15	72	22	3.27	480.00	146.67	0.95	313.33	46.67
13 (North)	0.21	135	29	4.66	642.86	138.09	0.99	195.24	23.81
14 (North)	0.20	98	21	4.67	490.00	105.00	0.82	135.00	15.00

Resource dispersion and dog numbers:

Garbage availability demonstrated significant positive correlations with both individual pack size ($r = 0.563$, $p = 0.036$) and overall dog density ($r = 0.601$, $p = 0.023$), indicating that neighbourhoods with greater waste availability supported both larger packs and higher densities of FRDs. This pattern aligns with resource-based predictions of animal population dynamics: where anthropogenic food subsidies are more abundant, dogs can maintain larger social units and achieve higher population densities. Feeding infrastructure showed a particularly strong positive correlation with pack density ($r = 0.856$, $p < 0.001$), indicating that areas with concentrated, regularised human feeding practices harboured significantly more packs per unit area. This relationship was substantially stronger than the garbage availability correlation, suggesting that the predictability and spatial concentration of intentional human provisioning—rather than incidental waste availability—is the primary driver of pack density across Delhi's urban gradient. Where communities engaged in ritual or regular feeding practices, FRD packs achieved their highest densities, compressing their territorial requirements in response to reliable, concentrated food sources. This relationship suggests that where communities engaged in regular, spatially concentrated feeding practices, FRD packs compressed their territorial requirements and increased their density—a mechanism consistent with optimal foraging theory predictions.

Notably, pack density demonstrated a significant negative correlation with adult sex ratio ($r = -0.589$, $p = 0.027$), indicating that areas with the highest pack densities, consequently supported by enormous food subsidies, exhibited male-biased sex ratios among adult dogs. Given the modest sample size (n=14 sampling units), these correlations should be interpreted as preliminary findings requiring validation in larger, independently sampled datasets. Time-activity budget observations revealed that vehicular and pedestrian traffic intensity significantly constrained FRD activity and spatial use. In high-traffic areas, dogs exhibited avoidance behaviour, selectively occupying refugia including spaces beneath/atop parked vehicles, building alcoves, and sheltered nooks that minimised exposure to traffic and human interference. Dogs in these high human and vehicular-traffic zones remained predominantly inactive during peak traffic periods, with activity increasing only during off-peak hours (11 pm - 07 am) or in sheltered locations where human and vehicular disturbance was minimal (Fig. 1. This pattern suggests that urban infrastructure and traffic dynamics function as significant ecological stressors, substantially limiting the behavioural repertoire and spatial accessibility of FRD populations.

In marked contrast, FRDs inhabiting areas with reliable human provisioning and minimal traffic disturbance exhibited substantially higher activity. A case study from *Moti Nagar* exemplifies this pattern: a residential block backyard (~800 m²) that received regular ritual feeding harboured three distinct dog packs totalling 19 individuals. Dogs within this feeding-provisioned area displayed active foraging, social interaction, and territorial patrol behaviours throughout 24-hr diel cycles. Such dogs exclusively dependent on ritual feeding in specific localities with low traffic exhibited notably heightened territorial aggression in response to stranger entry, displaying aggressive vocalisations and approach behaviours toward unfamiliar humans regardless of time of day.

Rather than simply affecting FRD abundance, ritual and opportunistic feeding by residents appears to fundamentally reorganise pack social structure and spatial distribution. From a management perspective, this finding indicates that interventions targeting feeding infrastructure—whether through formalised feeding programmes, restrictions on public feeding, or integration of feeding with sterilisation campaigns—may represent tractable levers for modulating pack density and territorial stability in ways that species-specific interventions (e.g., targeted removal) alone cannot achieve (Fig. 1). Below, we pair the correlations with qualitative data from semi-structured interviews to strengthen the interpretation beyond descriptive statistics.

S.1.5. Ethnographic insights from Delhi's multispecies co-existence

Humans and dogs

(i) *Recognition, Familiarity, and Differential Treatment*

All interviewees who engaged in regular dog feeding (n=35, excluding targeted ethnographic participants) reported that provisioned dogs recognised them reliably—either by visual appearance, distinctive vocalisations, or movement patterns. This recognition created differentiated spatial and social geographies within ostensibly shared urban spaces. Notably, others frequenting these same localities—including ragpickers, delivery personnel, and transient workers—expressed marked disdain toward provisioned dogs, attributing greater aggression to regularly fed animals. This perception, whether empirically accurate or not, fundamentally shaped how different urban residents navigated shared spaces and interpreted dog behaviour.

> *They guard this area because she feeds them. Dogs from the other lane also come here to eat, though I do not feel much attachment to them. They do not let random people enter the street. But we have to make rotis for them, before we cook for ourselves.*

> *At our temple, when kirtan used to happen, one dog would come and sit with us for the entire kirtan. We would give him prasad and then he would leave. Every being has sense* - A young female explaining how another girl feeds dogs on a daily basis and dogs from the lane and other lanes recognise her and come for food.

A priest from the temple at *Shastri nagar* pointed out how dogs are familiar with religious gatherings and sit until it is over to request *parasad* (food). These differential perceptions created what we term a geography of recognition and alienation: spaces transformed by consistent provisioning became socially and affectively loaded for some residents (feeders) while remaining sites of anxiety and avoidance for others (non-feeders). People who visited different parts of the city as part of daily routines—commuting to workplaces, collecting waste, making deliveries—encountered unfamiliar dogs in unfamiliar territories. Without the recognition relationship established through consistent feeding, these transient visitors experienced dog encounters as unpredictable and potentially threatening, generating uncertainty about appropriate behavioural responses when dogs approached. This created what anthropologists term "interactional friction": the inability to establish mutual recognition and appropriate social scripts for encounter, against the backdrop of prevalent urban conundrums in tropical cities that are socio-cultural agglomerates.

(ii) *Behavioural Adaptation and Perceived Risk*
Interviewees revealed individual strategies for managing perceived dog-related conflict risk. Residents expressing fear of dogs employed two primary coping mechanisms: **spatial avoidance** (selecting routes and times that minimised dog encounters) and **carrying defensive implements** (sticks, stones, or other objects for protection). Older adults were particularly affected, reporting that perceived dog-conflict risk in their neighbourhoods significantly restricted their daily mobility and social activities, contributing to feelings of isolation and constraint.

> *I do not go to the south side of 56 bigha-park anymore because of the dogs near the exit corner (middle aged female), or, I now leave the house only in the morning when the dogs are sleeping for my morning walk (an aged male)*

People with prior negative dog encounters—bites, chasing, or threatening approaches—demonstrated escalated defensive responses toward dogs more broadly, suggesting that individual negative experiences generalised into category-level avoidance or hostility. Over time, such interactions created feedback loops: prior negative encounters increased human aggression or avoidance toward dogs, which in turn intensified dog defensive or aggressive responses. This dynamic, though documented through self-report rather than direct behavioural observation, illustrates how human-dog conflict generates self-reinforcing cycles rather than discrete incidents (Fig. 1).

(iii) *The Failure of Population Control Approaches*
Current anti-birth control (ABC) programmes in Delhi—which primarily focus on sterilisation and neutering to reduce population growth—substantially underestimate the complexity of human-dog coexistence. These programmes operate under a simplified model: population size drives conflict, therefore reducing population size reduces conflict. However, our ethnographic data reveal a fundamentally different ecological and social reality: **the dynamics of human-dog interaction are constantly negotiated and renegotiated, making generic, one-size-fits-all interventions ineffective**. Interview data revealed substantial and widespread resident opposition to ABC practices. This opposition stemmed from three distinct, though sometimes overlapping, concerns:

A. **Cultural and Spiritual Concerns:** Some interviewees perceived street dogs as integral to the urban landscape, describing them in terms of familiarity, protection, and even spiritual significance consistent with certain Hindu philosophical traditions emphasising care for all sentient beings. Sterilisation was experienced as interference with the natural order or even as cruelty.

   We live with and depend on them. They can sense evil spirits before anyone else.

   We feed these dogs as our moral and spiritual duty. God is watching. These voiceless beings have no one else. Their presence helps keep us safe and creates a positive environment.

Every being has senses. They still carry memories from their past lives. Humans are the ones with corruption in their nature. Dogs live according to the laws of nature.

B. **Logistical and Practical Concerns:** Residents raised valid concerns about the feasibility of large-scale sterilisation implementation in densely populated Delhi: inconsistent capture and handling procedures, inadequate post-operative care and monitoring infrastructure, and the practical difficulties of identifying and tracking individual dogs across mobile, interconnected populations. The complexity of managing street dog populations in urban areas with constrained municipal resources made systematic ABC programmes appear unrealistic.
C. **Ethical and Welfare Concerns:** Interviewees engaged in sophisticated ethical debates about human responsibility and animal welfare, questioning whether large-scale surgical intervention—however well-intentioned—represented an appropriate response to urban coexistence challenges. These discussions often foregrounded the agency and welfare of the dogs themselves, rather than framing them purely as problems to be managed. These objections collectively highlighted the intersection of human values, urban ecology, and animal welfare—a reality that standardised population control programmes systematically overlook.

Here, they do dog surgery and leave the dogs in a poor state. Who gives them the right to take away dogs' reproductive rights? Most of them become abandoned like this, and this dog came here and started living around.

(iv) *Complex Lifeworlds: The Rohini Case*
A particularly illuminating case emerged from interviews with residents in the outskirts of Rohini, a northwestern Delhi suburb, revealing the complexity of simultaneous human attachments to and conflicts with dogs. One family described maintaining a deep emotional bond with their neighbourhood street dogs, caring for and provisioning them as integral members of their extended household. Paradoxically, these same residents experienced genuine predation threat: feral dogs, distinct from their familiar provisioned companions, occasionally preyed upon the calves and goats the family raised in their backyard.

We love our dogs that live with us (see, they have straps). They are like our children and we lock them with our high breed livestock inside the shanty. But the wild ones that come at night and attack our animals—those are different. We do not know them. These feral ones kill our livestock, as well as our dogs.

Our interviews and field observations revealed striking temporal and behavioral differentiation between street dogs and feral dogs at this location. During nighttime hours, when darkness provided cover from human scrutiny and intervention, street dogs and feral dogs converged in overlapping spatial and social domains. Feral dogs appeared to integrate, however temporarily, into the communal social dynamics established by street dogs—participating in collective foraging and social interactions. However, during daylight hours, behavioural divergence became pronounced: feral dogs retreated to the fringes of human habitation, scavenging from garbage piles while notably abstaining from the affiliative interactions (tail-wagging, approach, vocalisation) typical of socialised street dogs. This temporal and behavioural differentiation suggests that feral and street dog populations, despite their genetic proximity, occupy fundamentally different ecological and social niches within the same urban space.

At night, you can not tell our dogs and the wild dogs apart. They often mix together looking for food. But in the morning, the wild ones run away while our dogs stay.

This case exemplifies a critical insight: human-dog coexistence in tropical cities is not a binary of "conflict" versus "coexistence," but rather a **complex, multiplex set of simultaneous relationships** ranging from deep affection and care to predation threat and economic loss. Individual humans maintain differentiated relationships with distinct dog populations (street vs. feral, known vs. unknown), and their responses to urban dog presence reflect these distinctions. Generic management approaches that homogenise all FRDs as "problem animals" requiring control fundamentally misrepresent the lived complexity of these urban worlds (Fig. 1).

The divergence continuum in behavioural repertoire of street and feral dogs showcases how ecological, physical and social boundaries mediate coexistence. While both shared the urban periphery environment, their interactions were fundamentally tempered by feral dogs' reduced dependence on human affiliation. As night fell, feral dogs retreated into darkness, establishing resting sites 200-300 meters from artificial light sources—a spatial choice reflecting their fundamentally different relationship to human niche. Feral dogs sought solace in darkness and distance, while street dogs remained proximate to human settlements and artificial illumination. The contrasting behavioural and ecological patterns of street and feral dogs underscore the negotiation of space, resources, and relationships, variably shaped from Delhi's core to its urban periphery.

(v) Toward Dynamic, Contextually-Sensitive Understanding

These ethnographic findings collectively demonstrate that effective human-dog conflict mitigation requires abandoning simplistic, population-centric models in favour of approaches that centre the **dynamic ecology of daily human-dog interaction**. Understanding conflict requires attention to: (a) how recognition and familiarity mediate human responses to dogs; (b) how individual experiences generate behavioural feedback loops; (c) how cultural values shape acceptance of human intervention; (d) how spatial and temporal heterogeneity creates multiple, coexisting human-dog relationships; and (e) how marginalised communities bear disproportionate conflict costs while having minimal voice in management decisions. Only by honouring this complexity can urban planning and dog management move beyond reactive, often counterproductive interventions toward genuinely coexistent futures.

(vi) Urban Architecture as Ecological Constraint: The Unique Case of South Asian megacities

Delhi's dense, contiguous urban fabric creates a distinctive ecological matrix fundamentally shaping FRD behaviour and human-dog encounters. Unlike sprawling cities with fragmented development, or rural-urban peripheries with interspersed farmland and natural habitat, Delhi's architectural configuration—characterised by minimal/no gaps between residential structures and high building density—necessitates that street dogs rely almost exclusively on established roadways as primary nodes of movement, resource access, and shelter. Roads and streets function not merely as conduits but as **veritable territories and survival corridors**, shaping not only dog mobility patterns but determining access to critical resources: food derived from human interaction and urban refuse, suitable reproductive partners, and viable shelter zones. This reliance on road networks and constructed spaces invariably increases encounter frequency between urban canines and human pedestrians. The spatial coalescence of dogs and humans on Delhi's thoroughfares meets constant change in resource quality, quantity, predictability, and spatial distribution—becoming a crucible of selective pressures that likely shape dog behavioural responses (Fig. 1).

> *These three dogs stay here, near the Moti Nagar market dairy. They get food from there because people feed them things like paneer, and otherwise I also give them food.*

We learnt that some dogs approach and engage with pedestrians seeking food, while few chase and snatch food; others maintain distance or display defensive behaviours; still others appear largely indifferent to human passage. This behavioural heterogeneity reflects differential histories of positive, neutral, and negative encounters with humans—histories that are spatially structured by consistent feeding patterns, traffic intensity, and community attitudes.

(vi) The Architectural Choreography of Urban Coexistence

The unique structural configuration of Delhi's urban matrix fosters a multitude of distinctive scenarios in which **architecture, resources, and interspecies interaction sculpt the behavioural landscape** of FRD populations. The city's street dogs are simultaneously moulded by and actively mould this urban choreography: they navigate the constraints and possibilities imposed by Delhi's physical form while their movement patterns, territorial choices, and resource use reshape the social and ecological character of specific streets and neighbourhoods. The daily pursuit of survival, reproduction, and territoriality unfolds against the backdrop of continuous negotiation with human populations. This architectural-ecological coupling reveals that street dog behaviour cannot be understood through population-level metrics (density, pack size, sex ratio) alone (Fig. 1). Rather, these population patterns emerge from daily spatial negotiations within Delhi's specific urban form.

In *Moti nagar* market street with shops, FRDs were visible after 10 pm, very aggressively defending their spots frequently associated with feeding trays. But the residential lanes with no shops had fewer dogs and they seemed calmer. In the absence of architectural features that disallowed FRDs to seek refuge, dogs sat atop cars. This social-ecological and architectural perspective reframes the "dog problem" from a question of animal behavior or population control to a question of urban design, social-ethics and planning: *How do we design cities that facilitate multispecies coexistence rather than conflict*? *How can we reshape infrastructure, traffic patterns, cultural expressions and food systems to enable safer, more equitable encounters between humans and the canine populations that co-inhabit urban spaces*?

Human-Macaque Coexistence case at Dr B R Ambedkar University Delhi

(i) *Ecological Context and Displacement Intervention*

AUD campus is situated within a landscape of long-term macaque occupancy, embedded in the historically macaque-saturated areas surrounding Kashmere Gate and Old Delhi Railway Station. This region, characterised by age-old markets, medieval architecture, dense commercial spaces, and numerous religious sites, has sustained rhesus macaque populations for decades or potentially centuries, providing consistent ecological and infrastructural resources. Prior to intervention, 148 ± 6 macaques (based on $n = 5$ independent counts using a double sampling method) occupied the AUD campus and immediately adjacent areas, utilising institutional buildings, green spaces, and a historic *Hanuman* temple where predictable religious provisioning occurred, including a feeding peak on Tuesdays and Saturdays (auspicious *Hanuman* days) (Fig. 2). In response to escalating human-macaque conflicts, approximately 50 individuals were captured using baited cage traps and translocated in eastern Delhi. Despite this substantial removal, macaque numbers returned to pre-intervention levels within one month, demonstrating rapid recolonisation driven by the campus's position within a broader, saturated macaque habitat matrix. The following ethnographic insights, derived from semi-structured interviews with 30 campus stakeholders (22 security guards, 5 faculty members, 3 administrative staff) conducted between September 2023 and December 2024, illuminate the human dimensions of this displacement intervention and the complex social negotiations underlying human-macaque coexistence (Fig. 2).

Differential Vulnerability: (Security Guards as Primary Conflict Victims) Security guards—occupying lower-wage, outdoor positions with limited autonomy over work location and timing—emerged as the stakeholder group experiencing the most frequent and severe negative encounters with macaques. Guards reported that macaque aggression was not random but rather **strategically targeted**. Macaques appeared to recognise and selectively approach guards when the latter were positioned in spatially constrained locations—narrow corridors between buildings, dead-end staircases, or isolated guard posts with limited escape routes/without sticks or catapult for self defense. In these contexts, guards described feeling cornered and vulnerable due to threat behaviours (open-mouth threats, lunging, vocalizations), and in some instances physical contact (grabbing, biting).

> *When I am alone at the back gate and the monkeys come, I have nowhere to go. They know this. The alpha male always comes when I am checking the narrow entrance. He knows I can't run from there.*

Faculty members, who spent most time in enclosed offices and had greater control over movement timing and routes, reported typically being attacked at specific locations. This differential vulnerability underscores how **occupational position and socioeconomic status mediate conflict risk**: those with least workplace autonomy and highest exposure to outdoor spaces bear disproportionate costs of macaque presence.

I see the monkeys from my office window but they rarely bother me inside the buildings. When I need to leave, I just wait until they move away, or I call the guards for help.

(ii). *Temporary Relief and Return to Baseline Conflict*
Interviewees consistently reported that the displacement intervention provided only **short-term, illusory relief** from human-macaque conflict. During the first 7-10 days following macaque removal, campus stakeholders noted a marked reduction in macaque presence and encounters. However, this relief proved ephemeral. Within 2-3 weeks, macaque numbers and encounter frequencies returned to pre-intervention levels. More troublingly, several respondents perceived that **macaque aggression either returned to baseline levels or intensified** following recolonisation. The perception of increased post-displacement aggression, whether objectively accurate or not, suggests a potential unintended consequence of displacement interventions. Recolonising macaques—potentially dispersers from neighboring troops unfamiliar with campus human populations and resources—may exhibit different behavioural profiles than the displaced resident population. Alternatively, the disruption of established human-macaque recognition relationships through population turnover may have increased uncertainty on both sides, generating more frequent agonistic encounters as new macaques and resident humans renegotiated behavioural scripts for coexistence (Fig. 2).

(iii) *The Loss of Langurs and the Invention of "Monkey Chasers"*
Administrative staff interviews revealed a remarkable history of management approaches reflecting changing ecological realities and regulatory environments. Prior to 2012, AUD and surrounding institutions employed **live *Hanuman* langurs (*Semnopithecus* spp.)** as biological deterrents to macaque presence. Common langurs and rhesus macaques are sympatric species with complex competitive relationships: langurs, being larger-bodied and socially cohesive, can displace macaque troops through territorial defense and interspecific aggression. The practice of employing captive langurs to "chase" macaques from human spaces capitalised on this natural interspecific competitive dynamic.

In the early years at AUD, we had a langur with its keeper on campus. The macaques would disappear immediately when they heard/saw the langur. But it was discontinued in 2012.

However, following legislative intervention by animal welfare organizations (notably PETA) around 2012, the use of captive langurs for macaque control was discontinued on ethical and welfare grounds. This regulatory change created a management vacuum: langurs had been effective deterrents, but their use was now legally or ethically untenable. In response, the Municipal Corporation of Delhi (MCD) developed an innovative, if somewhat absurd, alternative: trained "monkey chasers"—human workers trained to imitate *langur* physical appearance and/or vocalisations. This practice has been documented in a bollywood movie, *Eb, Alley, Oo,* produced by Anurag Kashyap. These monkey chasers wore black costumes or carried props to simulate langur presence and produced vocal mimicry of langur alarm calls, attempting to trigger macaques' evolved competitive avoidance responses (Fig. 3).

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