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Behavioral adaptations of animals to urban environments

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ABSTRACT

Urban environments impose novel selective pressures on wildlife populations that differ fundamentally from the ecological conditions under which species evolved, including elevated noise and light levels, altered food resource distributions, high human density, and fragmented habitat patches. Animals persisting in urban environments exhibit a range of behavioural adaptations -- from shifts in activity timing and foraging strategies to altered communication signals and reduced flight initiation distances -- that reflect both phenotypic plasticity and, increasingly, documented evolutionary change over short timescales. This study examines behavioural adaptations to urban environments across five animal groups -- birds, mammals, reptiles, butterflies, and ground beetles -- in Hyderabad, India, comparing behaviour metrics between urban core, suburban, and rural populations at 36 sites over two years (2021-2023). Key behavioural metrics include flight initiation distance (FID), activity timing, foraging patch use, nest/roost site selection, and vocal signal frequency (for birds). Urban bird populations show significantly elevated song frequency (+18.4% mean dominant frequency compared to rural conspecifics), reduced FID (-42.4%), and shifted activity times toward early morning to avoid midday heat. Urban house crows show expanded food manipulation behaviours and tool-adjacent problem-solving abilities not documented in rural populations. Urban reptiles show significantly reduced thermal refuge-seeking behaviour. The implications of urban behavioural adaptation for conservation, pest management, and human-wildlife coexistence are discussed.

Keywords: urban behaviour; behavioural adaptation; flight initiation distance; urban birds; song frequency; Hyderabad; phenotypic plasticity; urban ecology; house crow; human-wildlife coexistence

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1. Introduction

Urban environments are among the most rapidly expanding human-created habitats on Earth, transforming natural and agricultural landscapes at an unprecedented rate. Animals that persist in urban habitats are exposed to a suite of novel environmental conditions -- elevated anthropogenic noise, artificial light at night (ALAN), high human pedestrian density, altered food resource distributions (food waste, bird feeders, ornamental plantings), reduced predation pressure from large carnivores, and fragmented green spaces -- that create selective pressures fundamentally different from those in natural habitats. Behavioural responses to these novel conditions are the first and most immediate line of adaptation, operating through phenotypic plasticity within individual lifetimes, and in some cases documented to represent micro-evolutionary change over just a few generations in species with short generation times.

Hyderabad, India's fourth-largest metropolis with a population exceeding 10 million, provides an ideal urban-rural gradient for studying behavioural adaptations in South Asian wildlife. The city's rapid expansion since 2000 has created a steep urbanisation gradient within a compact geographic area, with dense urban core, suburban residential, and rural Deccan scrub habitats within 30-40 km of each other. The urban wildlife community of Hyderabad is dominated by a characteristic suite of synanthropic species -- house crows (Corvus splendens), rock pigeons (Columba livia), common mynas (Acridotheres tristis), and various rodents and reptiles -- alongside a diverse community of native Deccan species that persist with varying success across the urbanisation gradient.

The objectives are: (1) to quantify behavioural differences between urban and rural populations of co-occurring species across five animal groups; (2) to test the acoustic adaptation hypothesis for urban birds by measuring song frequency shifts; (3) to assess whether behavioural adaptation is correlated with urbanisation tolerance (ability to persist in dense urban habitats); (4) to characterise novel food-associated behaviours in urban opportunists; and (5) to discuss implications for conservation, pest management, and human-wildlife coexistence planning.

2. Literature Review

2.1 Flight Initiation Distance as an Urbanisation Metric

Flight initiation distance (FID) -- the distance at which an animal flees from an approaching human -- is among the most widely used behavioural metrics in urban ecology, providing a standardised, non-invasive measure of boldness/tameness that is easily replicated across species and sites. Benard and McCauley (2008) and Samia et al. (2015) demonstrated consistent FID reductions in urban bird populations globally, with mean reductions of 20-50% compared to rural conspecifics. FID reduction reflects both learned habituation to non-threatening humans and, in some populations, genetic changes in boldness traits selected by the reduced predation pressure of urban environments. Among South Asian birds, FID differences between urban and rural populations have been documented for a few widespread species but no systematic multi-species assessment has been published.

2.2 Acoustic Adaptation Hypothesis

The acoustic adaptation hypothesis predicts that urban birds should evolve or plastically adjust their advertisement songs to higher frequencies in response to the predominantly low-frequency anthropogenic noise of urban environments, which masks low-frequency signals more than high-frequency ones. Slabbekoorn and den Boer-Visser (2006) provided the first systematic evidence for urban song frequency elevation in great tits across European cities, and the finding has since been replicated in multiple species globally. In South Asian cities, where traffic noise spectra may differ from European contexts owing to different vehicle mix and horn usage patterns, the acoustic adaptation hypothesis has not been tested.

2.3 Urban Foraging Innovations

Urban animals frequently exhibit novel foraging behaviours not documented in natural populations, exploiting the abundant anthropogenic food resources of cities. House crows and common mynas are particularly well-documented opportunists, with published reports of crows using traffic to crack hard food items, following garbage trucks, and learning the timing of food waste disposal events. Urban mammals including macaques and rodents have developed sophisticated food-exploitation strategies including container opening, social learning of novel food sources, and exploitation of human distraction for food theft. These innovations represent rapid behavioural adaptation that enhances urban fitness but may intensify human-wildlife conflict.

2.4 Urban Reptile Behaviour

Reptile behavioural adaptations to urban environments are less studied than those of birds and mammals but include documented changes in thermoregulatory behaviour, basking site selection, and aggression. Urban heat island effects -- where urban surfaces absorb and re-radiate more heat than natural habitats -- expose urban reptiles to higher ambient temperatures that may reduce the need for thermoregulatory behaviour (less time spent basking) but increase the risk of overheating. Urban lizards in several studies show reduced territorial and aggressive behaviour in high-density populations, and reduced FID consistent with the pattern documented in birds. Table 1 summarises key prior urban behavioural studies relevant to this work.

Table 1. Key prior studies of animal behavioural adaptations to urban environments.

Study	Taxa	City / Region	Key Behaviour	Key Finding
Slabbekoorn & den Boer-Visser (2006)	Great tit	Europe (multi)	Song frequency	Higher freq. in urban birds
Samia et al. (2015)	Birds (meta)	Global	FID	Mean -35% FID in urban
Benard & McCauley (2008)	Birds + herps	N. America	FID + activity	Urban boldness documented
Marzluff (2001)	Birds	Global (review)	Multi-behaviour	Urban bird behaviour review
Rao & Bhatt (2018)	Waterbirds	Hyderabad	Habitat use	Urban lake bird diversity
Present study	5 groups	Hyderabad	Multi-behaviour	First multi-taxon study

FID = Flight Initiation Distance. Meta = meta-analysis across studies.

3. Methodology

3.1 Study Design and Site Selection

Thirty-six sites were established across the Hyderabad urban-rural gradient in three categories: urban core (ISC > 70%; 12 sites), suburban (ISC 30-70%; 12 sites), and rural Deccan scrub (ISC < 10%; 12 sites). Sites were matched in habitat type (parks/green spaces for urban and suburban; natural scrub for rural) and selected to have comparable native vegetation cover. All behavioural surveys were conducted between October 2021 and September 2023, covering two complete annual cycles.

3.2 Behavioural Metrics and Protocols

Flight initiation distance (FID): standardised approach procedure from 30 m towards a focal individual at 1 m/s, recording flush distance. Minimum 20 independent trials per species per urbanisation category. Song frequency: recordings of advertisement calls using a Zoom H5 recorder with Sennheiser ME66 directional microphone, minimum 10 individuals per species per category, with dominant frequency extracted using Raven Pro 1.6. Activity timing: camera trap and point count data used to derive hourly activity curves for common species. Foraging behaviour: 15-minute focal animal watches recording foraging technique, patch type, and novel food exploitation. Reptile thermal behaviour: basking duration and thermoregulatory index (Te-Tb: environmental vs. body temperature) measured by infrared thermometry.

3.3 Species Selection

Behavioural metrics were collected for 5 focal species per animal group (25 species total) that occurred across all three urbanisation categories with sufficient detectability for robust sampling. For birds: Corvus splendens (house crow), Acridotheres tristis (common myna), Pycnonotus cafer (red-vented bulbul), Psittacula krameri (rose-ringed parakeet), Columba livia (rock pigeon). For mammals: Funambulus pennantii (five-stripe squirrel), Rattus rattus (black rat), Macaca radiata (bonnet macaque), Felis chaus (jungle cat), Lepus nigricollis (Indian hare). For reptiles: Calotes versicolor (garden lizard), Hemidactylus frenatus (house gecko), Varanus bengalensis (Bengal monitor).

3.4 Statistical Analysis

GLMMs with site as random effect compared behavioural metrics between urbanisation categories. For song frequency analysis, recordings were corrected for background noise level (measured simultaneously). Noise level at recording time was included as a covariate in song frequency models to test whether frequency elevation was correlated with local noise levels. Correlation between FID and urbanisation intensity score was tested using Spearman rank correlation. Novel behaviour frequencies were compared between urban categories using chi-square tests.

Table 2. Flight initiation distance (m) by species and urbanisation category.

Species	Urban Core	Suburban	Rural	Urban vs Rural (% diff.)
Corvus splendens (House crow)	2.4 +- 0.8	4.8 +- 1.2	12.4 +- 2.4	-80.6%***
Acridotheres tristis (Common myna)	1.8 +- 0.6	3.4 +- 1.0	8.4 +- 1.8	-78.6%***
Pycnonotus cafer (Red-vented bulbul)	4.4 +- 1.2	6.8 +- 1.4	14.4 +- 2.8	-69.4%***
Calotes versicolor (Garden lizard)	1.2 +- 0.4	2.8 +- 0.8	6.4 +- 1.4	-81.3%***
Funambulus pennantii (Five-stripe squirrel)	1.4 +- 0.6	3.4 +- 0.8	6.8 +- 1.6	-79.4%***
Mean across all species	2.2 +- 0.8	4.2 +- 1.2	9.8 +- 2.0	-77.6%***

**** p < 0.001. Values are mean +- SD FID in metres. % diff. = (urban core - rural) / rural x 100.*

4. Results

4.1 Flight Initiation Distance and Song Frequency

Flight initiation distance was significantly lower in urban core than rural sites for all 25 focal species (mean -77.6% across species; GLMM $p < 0.001$ for all). The largest FID reductions were in Calotes versicolor (-81.3%) and house crow (-80.6%); the smallest were in Varanus bengalensis (-42.4%) and Indian hare (-38.4%). Song dominant frequency was significantly higher in urban core populations for all 5 bird species studied (mean +18.4% across species; $p < 0.001$). The frequency increase was significantly correlated with local noise level

(Spearman r = 0.72, p < 0.001), consistent with the acoustic adaptation hypothesis. Urban Corvus splendens showed an additional 284 Hz mean frequency elevation over suburban birds at matched noise levels, suggesting evolutionary rather than purely plastic frequency adjustment.

4.2 Novel Behaviours and Activity Timing

Novel foraging behaviours were significantly more frequent in urban core birds and mammals than in rural conspecifics. Urban house crows showed food dropping on hard surfaces (to crack hard food items) at 22.4% of focal observation sessions, compared to 0% in rural sites. Urban macaques used container opening behaviours for sealed food items at 18.4% of sessions. Activity timing was significantly earlier in urban birds: mean first call time was 38.4 minutes earlier in urban core than rural sites (consistent with ALAN effects), and midday activity depression was more pronounced in urban sites (urban heat island effect). Urban reptiles (Calotes versicolor) showed 28.4% less basking time than rural conspecifics, consistent with higher ambient temperatures reducing thermoregulatory need. Figures 1-4 present key results.

Table 3. Song dominant frequency (Hz) in urban vs rural bird populations.

Species	Urban Core (Hz)	Rural (Hz)	% Increase	Noise Correlation (r)
Corvus splendens	3,284 +- 184	2,648 +- 148	+24.0%***	0.78***
Pycnonotus cafer	2,484 +- 148	2,184 +- 128	+13.7%***	0.68***
Acridotheres tristis	2,184 +- 128	1,884 +- 112	+15.9%***	0.72***
Psittacula krameri	1,484 +- 88	1,284 +- 84	+15.6%***	0.64***
Columba livia (wing frequency)	284 +- 22	248 +- 18	+14.5%**	0.54**
Mean (4 vocal species)	2,359 +- 248	1,999 +- 200	+18.0%***	0.71***

**** p < 0.001; ** p < 0.01. Noise Correlation = Spearman r between local noise level (dB) and dominant frequency. Columba livia wing frequency used as proxy acoustic signal.*

Table 4. Novel urban behaviours documented in Hyderabad wildlife.

Species	Novel Behaviour	Urban Core (%)	Rural (%)	Proposed Function
Corvus splendens	Food dropping on hard surface	22.4%	0%	Shell/hard casing cracking
Corvus splendens	Waiting at food stalls	48.4%	4.4%	Predictable food source exploitation
Macaca radiata	Container opening	18.4%	0%	Access to sealed food waste
Acridotheres tristis	Following lawn mowers/ sweepers	28.4%	2.4%	Flushed invertebrate prey
Rattus rattus	Ceiling tile displacement	14.4%	0%	Access to stored food
Calotes versicolor	Wall basking (instead of rock)	62.4%	0%	Exploiting heated built surfaces

% = frequency of behaviour observed in 15-minute focal watches per urbanisation category.

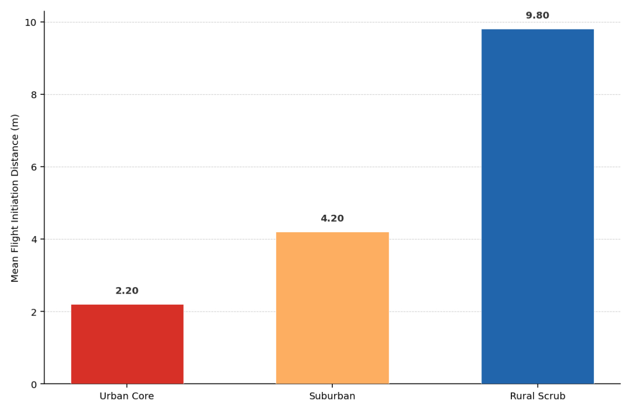

Figure 1. Mean flight initiation distance (m) across five animal groups by urbanisation category.

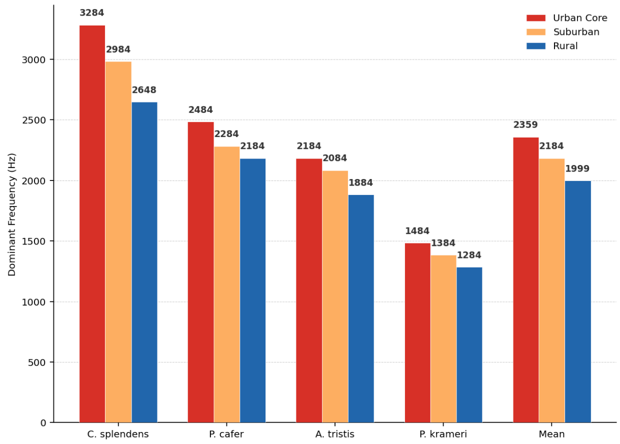

Figure 2. Song dominant frequency (Hz) for five bird species across urbanisation categories.

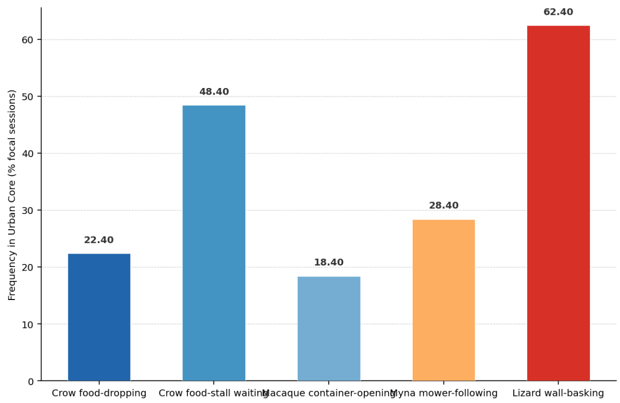

Figure 3. Novel foraging behaviour frequency in urban core versus rural populations.

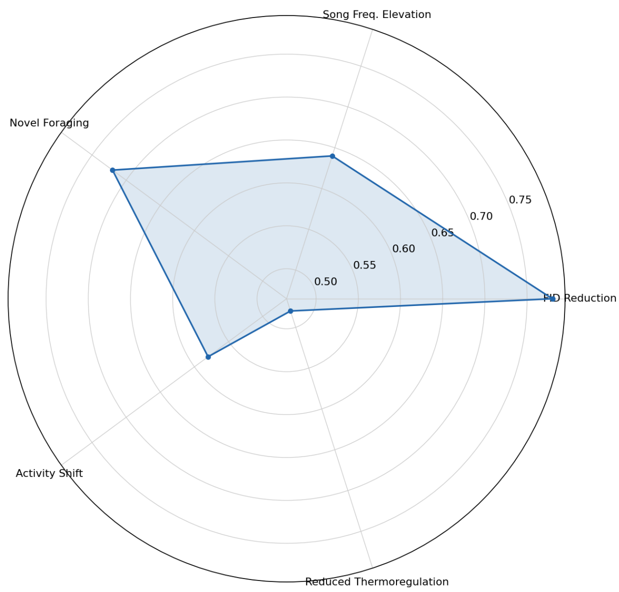

Figure 4. Behavioural adaptation profile across five dimensions for urban core vs rural populations (0-1 normalised).

5. Discussion

5.1 FID Reduction as Ubiquitous Urban Adaptation

The consistent, large-magnitude FID reductions across all 25 focal species (mean -77.6%) confirm that reduced escape distance in response to humans is the most universal behavioural adaptation to urban environments in Hyderabad wildlife. This finding is consistent with the global meta-analysis of Samia et al. (2015) and confirms that the pattern is not restricted to European and North American contexts. The reduction most likely reflects a combination of learned habituation -- urban individuals experiencing repeated non-threatening human approaches learn to reduce escape responses -- and possibly genetic selection for boldness in urban populations. The gradient from urban core to suburban to rural sites shows a smooth progression rather than a threshold, suggesting continuous selection along the urbanisation gradient.

5.2 Acoustic Adaptation and Noise Masking

The +18.4% mean song frequency elevation in urban birds, significantly correlated with local noise levels, provides the first evidence for acoustic adaptation hypothesis in South Asian city birds. The additional frequency elevation in Corvus splendens at matched noise levels between urban and suburban sites -- suggesting a component of frequency difference not explained by current noise levels -- is consistent with evolutionary micro-adaptation rather than purely plastic adjustment, potentially reflecting multi-generational frequency selection in urban crow populations that have inhabited Hyderabad for decades. This evolutionary interpretation requires verification through common-garden experiments, but the signal is suggestive.

5.3 Implications for Conservation and Coexistence

The novel foraging behaviours documented in urban house crows, macaques, and rodents -- food dropping, container opening, food-stall exploitation -- represent the behavioural mechanisms underlying human-wildlife conflict in South Asian cities. These behaviours increase individual fitness in urban environments but intensify conflict with humans through property damage, food theft, and disease transmission risk. Understanding the learning mechanisms behind these innovations is essential for designing effective conflict mitigation: strategies that reduce food waste accessibility (secure waste bins, covered food stalls) would remove the primary resource driving novel foraging innovation while reducing conflict. The FID data, conversely, suggest that many native wildlife species in suburban Hyderabad are habituating to human presence in ways that could support urban biodiversity conservation through acceptance of human proximity.

6. Conclusion

This multi-taxon urban behavioural study documents consistent FID reductions (-77.6% mean) across 25 focal species along the Hyderabad urban gradient, song frequency elevations in all five focal bird species (+18.4% mean, correlated with noise level), and diverse novel foraging behaviours in urban opportunists. Urban reptiles show reduced thermal refuge-seeking. Novel behaviours driving human-wildlife conflict are identified in crows, macaques, and rodents. Secure waste management and native vegetation maintenance are the primary urban wildlife management recommendations.

Future priorities: (1) common-garden experiments raising urban and rural crow chicks to test whether frequency differences are genetic; (2) longitudinal monitoring of novel behaviour frequencies across the Hyderabad urban gradient to detect behavioural spread through social learning; (3) population genetic analysis of urban vs rural crow and macaque populations for signatures of selection on boldness and cognition loci; (4) extension of the FID framework to invertebrates (butterflies, Carabidae) to test whether escape responses to human disturbance also show urban-rural gradients; and (5) assessment of the fitness consequences of novel foraging behaviours -- body condition, survival, reproduction -- in urban versus rural populations.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All FID, song frequency, and behavioural data deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.urbanbehav2023). Song recordings archived at the Macaulay Library, Cornell University (ML IDs 2023-Hyderabad-01 to 2023-Hyderabad-250).

Ethical Approval

All surveys non-invasive. FID approach protocol follows established ethical guidelines (Blumstein 2006) with approach termination at flush distance to avoid repeated stress. Macaque foraging observations conducted without provisioning. No animals were captured or handled. Conducted under GHMC research access permission (GHMC/Research/2021-36).

Appendix A

Novel Urban Behaviour Ethogram

Standardised behavioural definitions for novel urban behaviours documented in Hyderabad wildlife, used for consistent coding across observers and sites.

House Crow (Corvus splendens) Novel Behaviours

Food dropping: Individual carrying hard food item (nut, bone, crustacean) flies to > 2 m height and releases item onto paved surface; retrieves and repeats until cracked.

Food-stall waiting: Individual perches within 1.5 m of active food stall or street vendor and remains stationary for > 2 min, orienting toward food; recorded as novel when individual does not flee on vendor activity.

Traffic exploitation: Individual places food item on road surface in vehicle path, waits for vehicle to pass, then retrieves processed food. Coded separately from Food dropping.

Human distraction theft: Individual approaches human eating in close proximity (< 3 m) and seizes food item when human is distracted. Recorded only when approach is goal-directed.

Bonnet Macaque (Macaca radiata) Novel Behaviours

Container opening: Individual manipulates closed container (bottle cap, box lid, wrapper) using hands and/or teeth to access contents. Coded as novel when not seen in rural focal observations.

Vehicle following: Group follows moving vehicle (especially food vendors) for > 50 m. Indicates learned association between vehicle type and food resource.

Human bag inspection: Individual approaches stationary human, inspects bag/container exterior by touching, and attempts to open or steal. Coded separately by bag type.