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How do animals navigate the urban jungle? A review of cognition in urban-adapted animals

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Rapid urbanisation leading to habitat loss is a major problem for biodiversity conservation. While urbanisation negatively affects the survival of many species, some species are well adapted to the urban environment, often depending on humans directly or indirectly for food and shelter. Such animals show various behavioural adaptations to anthropogenic disturbance, and there are even examples of some exploiting humans for their own advantage. In this review, we use some of these examples to highlight how cognitive and physiological underpinnings of urban adaptation in some animals can help us to understand how they survive in the human jungle. We propose that more in-depth studies of urban-adapted species are necessary for nurturing biodiversity in the face of urbanisation, and building more sustainable cities for the future.

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Introduction

The physical and social environments of free-ranging and wild animals are unpredictable. This is especially true for urban habitats like cities wherein urbanisation and other anthropogenic activities have transformed key ecological conditions like habitat and food sources. Thus, they present novel conditions and challenges for animals, different from their natural conditions under which they have evolved. The ability to successfully respond to such conditions is dependent on behavioural flexibility and diversity of the animal [1]. Evidence for such behavioural characteristics has been found in multiple animals living in unpredictable and complex environments demonstrating different, and sometimes higher cognitive skills than those living in stable environments [2].

In the last 60 years, since Jane Goodall first observed termite fishing in chimpanzees at Gombe, interest in the cognitive abilities of nonhuman animals has grown manifold, and research has spanned across realms of cognition, as diverse as learning, tool use, language, numerosity expression and social cognition [3]. While majority of studies have been carried out in controlled lab environments or on captive and semi-captive species, cognition in the wild has been a steady presence in the field of cognitive research [4]. In their daily life, wild animals face numerous challenges like shifting food availability with changing seasons, prey-predator challenges, interacting and competing with conspecifics and other animals. Change in behaviour is one way in which animals adapt to new environmental conditions by memorising and learning from past experiences to hone and adapt their behaviours for subsequent experiences [5]. Such behaviourally adaptive animals will have advantages over behaviourally fixed individuals and will in turn contribute to the persistence and survival of their population. An example of such flexibility is seen in female elk learning to avoid human hunters by taking forest cover and lowering movement rate as they age, thus showing the propensity of learning from the mistakes of others. They also learn to differentiate between bow hunting and rifle hunting season with older female elk favouring rugged terrain during the bow hunting season for easier detection of hunters and to prevent stalking by them [6]. Other instances of such adaptation can be seen in a variety of situations like mating, foraging, and habitat selection.

One such environmental challenge in modern times is urbanisation. Urbanisation is a form of human-induced rapid environmental change (HIREC), bringing its own sets of challenges and benefits. On one hand, urban habitats suffer from loss of vegetation and tree cover, high human density, habitat fragmentation and patchy habitats due to man-made barriers like roads and railway corridors, predation, food scarcity due to dearth of native food sources, anthropogenic disturbances like noise, chemical contaminants and pollution. But, on the other hand urban habitats offer anthropogenic structures like houses, factories etc that serve as alternative, analogous sources of shelter like roof openings and pylons, warmer

conditions, novel and exotic food and food sources, high stability of these sources, and improved foraging conditions. While urbanisation often leads to a dramatic loss of species diversity, some organisms like birds, coyotes, and red foxes among others are able to adapt, and even thrive in certain urban habitats [7]. Animals that face cues and conditions that share some similarity with past experience often tends to perform better than animals that face fundamentally different, truly novel conditions in HIREC- altered environments. This is one of the reasons why generalist species having a larger behavioural repertoire and wider signal- response system, in most cases, tend to perform better in urban habitats than specialists [8]. Survival in the human jungle is a result of physiological, morphological and behavioural adaptations, and often involve cognitive abilities that enable the animals to sustain in a highly disturbed and altered environment [9]. In recent years, a growing interest in urban adaptation and animal cognition has led to research in the areas of animal response to anthropogenic cues and human-animal interactions.

One way in which animal cognition in the context of anthropogenic activities and cues is studied is through domesticated animals or human-socialised, human-reared wild animals. Although domestication and urbanisation may lead to certain similarities in animal behavioural repertoire like prolonged breeding season, decreased fear towards humans, and reduced corticosterone levels, both the processes are unequivocally different. Furthermore, domestication involves an evolutionary process in which animals are artificially bred and selected for human-useful traits that includes tameness and sociability towards humans. Urbanisation on the other hand brings those animals in close proximity to humans that do not have a life history of human supervision and do not necessarily have the evolutionary history of domestication. The ability to comprehend and respond to anthropogenic cues by animals borne of these two processes will differ substantially. Additionally, animals under direct human supervision or dependent on them directly may become trained or experience learning opportunities to anthropogenic cues frequently skewing their response away from an individual for whom such cues are novel or recent.

Another way of testing such cognitive paradigms has been through captive or laboratory-based studies. A study in 2018 found that a staggering 83.7% of all behavioural science experiments took place in captive or laboratory-based settings [10]. These studies have the advantages of having controlled environmental and internal factors that could have an effect on the cognitive performance of the animal at a given time. But they are limited in a variety of ways. These artificial environments remove animals from their natural settings and create disturbances in behavioural patterns and ecological conditions, for example, stress from altered grouping sizes, stress from isolated testing conditions, and atypically small territories. Furthermore, the effect of living in an artificial physical, perceptual, and social environment on the socio-cognitive development of animals and their resulting actions is still not fully known and cannot be generalised to wild or free-ranging populations. Captivity studies are also suggested to result in truncated or diminished capacities and behaviours under certain circumstances and lead to inaccurate results [11]. Interestingly, research has shown that noncaptive animals perform just as well as captive animals and show similar participation rates and performance improvements when both populations are tested on the same experimental methodology [12]. Increasingly scientists are realising that instead of bringing animals to testing centres, we should work towards taking the testing paradigms to the animals in their natural settings. The option of 'voluntary' participation of animals in cognitive testing is gaining traction among scientists [12]. The unique opportunities accorded for studying noncaptive animals on their own terms and in their natural environment are potential alternatives to more invasive methods of scientific investigation.

In this review, we put a spotlight on the behavioural and cognitive adaptions of untrained, nonhuman-socialised urban animals in their day-to-day interactions with the various components of an urban environment and their response to such novel challenges. Our focus is specifically on in situ research that has demonstrated the cognitive capacity of these animals and their ability to thrive in such an everchanging environment. We begin by briefly reviewing the cognitive, behavioural and ecological literature that examines the behaviour, abilities and adaptations of animals in the urban environment. Particularly, we attempt to combine and synergise findings from different sources examining the adaptations in behaviour and cognitive skills demonstrated by urban animals, thus presenting an animal-centric point of view, to tackle three core ecological factors when colonising and establishing a population in any new urban environment: food, shelter, and interaction with humans. We do not provide an exhaustive review on the topics but give an overview of the abilities displayed by urban animals and highlight the opportunities for further research present therein. Primarily, we have highlighted examples from research in the Global South for we feel that area is under-represented in urban wildlife cognitive research, and is a region that is undergoing rapid urbanisation in the present times. Additionally, we majorly highlight cognitive abilities of animals that have already had a long history of urban adaptation and exploitation as opposed to their 'wilder' brethren that have a more recent history of urban adaptation, and might be exploiting urban resources from the fringes. In the end, we discuss in detail the ways to act upon and improve on the

opportunities that may have been overlooked and the steps required to bring the cohabitation of humans and animals on an equal footing in the emerging urban ecosystem.

Cognition of free-ranging urban animals

Urban-adapted, free-living animals are the ideal model organisms to study the functional aspect of cognitive abilities centred around anthropogenic cues as they often come in contact with humans in different capacities. These animals exploit anthropogenic sources of food and shelter while also being persecuted by humans directly and indirectly for various reasons [13]. Living in human-dominated environments also brings with it other novel challenges unknown to animals in their evolutionary past like navigation around barriers in the form of roads and fences, elevated light and noise pollution. Successful response to these novel socio-ecological situations, as the cognitive buffer hypothesis states, is a product of larger brains which allow animals to adapt to environmental vagaries using novel behaviour [14]. This behavioural flexibility arises from a combination of different cognitive abilities like exploration, innovation, learning. This allows an animal to adapt efficiently using existing responses and strategies to variation in an environment without being constrained by instinctive, fixed behaviour [15]. A classic example of such explorative and innovative behaviour comes from great and blue tits in UK who learnt to recognise milk bottles as food source and figured out a way to prise open the wax board tops of the bottles to access the milk inside. Interestingly, this behaviour was much less prevalent in Ireland than in England where bottled milk was not a common delivery service in 1949. A similar innovative behaviour was reported from Miyagi Prefecture, Japan, where crows learnt to use cars as nut-crackers. The crows were observed to place the walnuts at spots where the cars were most likely to run over it or in front of stopped cars. Consistent with these observations supporting cognitive buffer hypothesis are the reports of urban animals having higher rates of innovation and problem solving than their rural counterparts [16] (But see, Johnson- Ulrich et al., 2021 [17]). Such cognitive abilities are influenced by neophilia, an attraction to novelty, an important trait for taking advantage of new resources in human-altered landscapes [18].

Food

Attraction and exploration of new food items are important skills to adapt to new environments. Newly arrived animals are often confronted with novel food, especially in urban habitats and must either adapt to the new opportunities or die of starvation. In fact, research has shown that species with higher feeding innovation and attraction rate are much more successful at colonising new areas [19]. Finding underutilised food sources and efficient novel resource use are useful in all four stages of colonising new environment: arrival, establishment, expansion and spread [8]. Individuals who show such adaptiveness are often seen to be bolder characterised by shorter novel stimuli exploration latencies and neophilia [8]. Such characteristics are often much more pronounced in urban animals than animals from less urbanised environments [20]. There are multiple advantages of adapting to an anthropogenic diet such as the availability of various high-calorie resource options which are reliable, easily accessible, digestible, and seasonally stable [21,22]. Access to human foods translates to more energy and thus increased foraging efficiency. This results in less time spent in foraging activities and more time for nurturing social interactions, thus leading to long-term fitness benefits [23].

Often times the diet of such urban animals is found to be majorly comprised of human food. Free-ranging grey langurs in Dakhineswar, India, a locality with high human interference and interaction with these animals, not only learnt to recognise human-provisioned, processed food items as an alternative to the natural food sources, but also preferred these over unprocessed natural food in a food-choice test [24]. Free-ranging dogs have spent their time in and around human settlements for millennia. They are especially interesting because although they have undergone domestication, their history of living independently, without human supervision or help precedes any known history of urbanisation. These dogs subsist on a carbohydrate-rich omnivorous diet, despite maintaining a preference for meat [25]. These dogs feed regularly from dustbins and garbage dumps and are able to classify cues in a way that allows them to discriminate between unpalatable items (leaf litter, rotten food) and edible food items [25,26]. Similar alteration in diet has been observed in scrub jays [27] and foxes [28] living in urban areas. In all the examples, the animals are able to survive by eating whatever is available to them. This is possible because of a generalised digestive system and show great flexibility in their diet depending on their location. Thus, the behavioural adaptations are possible because of existing physiological characteristics and evolutionary changes [29,30].

In addition to altering their diet to include anthropogenic food, the ability to adapt to novel challenges also extend to obtaining food. Caracals foraging in a risky landscape choose to reduce movement, prolong handling time and make use of vegetation cover to 'hide in plain sight', rather than using spatial or temporal partitioning to avoid human-associated risk altogether, unlike other urban carnivores [13,31], using their reddish-brown coat to camouflage in high-quality patches. On encountering humans they choose to remain stationary instead of running away showing a degree of habituation to human presence [31]. Free-ranging grey squirrels are able to

solve puzzle box tasks, even using counterintuitive methods, to obtain food, demonstrating a remarkable level of behavioural flexibility and persistence. The fact that the invasive grey squirrels performed better than the native red squirrels is proof of their better problem-solving abilities and one of the reasons of their success in colonising new areas. Such abilities are crucial for resource exploitation and survival [32]. Herring gulls in England are able to use local enhancement when foraging wherein they are able to use human behavioural cues as markers to indicate the presence and location of food [33]. In a testament to their cognitive abilities, bordering on guile, free-ranging long-tailed macaques were observed to first rob temple visitors of inedible items (sunglasses, bowl, etc.) and then use these objects as tokens to barter for food [34]. This opportunistic exploitation in a human-dominated environment is a spontaneous and enduring population-specific practice underscoring the macaques' abilities of economic behaviour, numerical judgement, delay of gratification, and social learning [35]. This association of humans as potential food sources is also demonstrated by the begging behaviour displayed by urban animals such as dogs [36], and gulls [37].

Shelter

Another evidence of the intrepidity of urban-dwelling animals are their use of man-made structures and adjacent areas as dens and shelters. Rapid urbanisation has caused the fragmentation of habitats for animals worldwide and loss of natural habitats. This results in declining of natural roosting and denning sites and has an impact on their breeding ecology, energy optimisation, and thus persistence within the urban environment [38]. Animals adapt to these changes by using different types of anthropogenic structures such as culverts, gardens, flood channels, sewers and buildings as alternative to natural shelters [13,39]. Even the intensely reclusive fishing cat was discovered to be prowling the ever-growing streets of Colombo, capering over roofs and stealing koi fish from swimming pools in 2015 [40]. In some cases, urban animals exclusively use anthropogenic structures. For example, studies on urban stone martens in USA [41] and great tits in Poland [42] found that 97% of the stone marten dens and 80% of the local tit populations were in buildings and vertical pipes of fences respectively. Small mammals like opossums [43] and badgers [44] make use of under floor spaces of buildings as denning sites. The rock honeybee, *Apis dorsata* is known to use architectural structures like eaves, balconies etc. of tall buildings as nesting sites [45]. These examples demonstrate the habituation of urban animals to anthropogenic infrastructure.

Often times these animals tend to select structures that closely resemble their natural habitats. Thus, common blackbirds in Hangzhou, China swap tall trees for tall buildings as nesting sites and large-spotted genets in KwaZulu-Natal, South Africa replace tree hollows with compartmentalised roofs, eaves and outbuildings [39,46]. Thus, the birds apply pre-existing skills to new but similar and predictable structures demonstrating behaviour flexibility. Such urban manifestation of pre-existing behaviour and knowledge can be observed in house sparrows and finches of Mexico City that incorporate cellulose cigarette butts into nest structures to act as arthropod repellents as an urban solution to the green plant materials used in the wild [47]. Adaptive use of anthropogenic materials such as plastic pieces and metal wires in nests were also observed in urban birds of Punjab, India [48]. While it has been theorised that the anthropogenic materials are used on account of their resemblance to natural materials with which the birds originally made their nests, studies on captive zebra finches have shown that they learn to assess the efficacy of the strength of artificial building materials and with increasing nest-building experience their preference for the optimum material is crystallised [49]. Thus, the use of certain anthropogenic materials in bird nests can be seen as action of intent meant to increase fitness rather than simplistic copying. This is further supported by multiple studies in noncaptive urban birds that show among other things that plastic in birds' nest has a signalling function, is used in an attempt to increase mating success, may strengthen the nest structure and building ease and may also be used as back-up material in case of paucity of natural materials. Taken together the adaptive behaviour of using anthropogenic materials in nest building serve as examples of the urban bird's cognitive abilities of learning through experience and innovation in the context of exploitation of novel resources and problem solving. Furthermore, the rapid pace of urbanisation means that spatial features or landmarks that served as cues for animals disappear and alter within the life span of animals. In such conditions, short-term memories of relevant resources need to be updated quickly with new information. Indeed, the suburban South Indian rock agama display quicker rates of learning and unlearning the location of safe refuges than those from rural areas [50].

There are multiple advantages of living near or in human habitations. In some cases, like red foxes [51] and free-ranging dogs [52] denning close to human settlements helps them to avoid competition with other mesocarnivores and predation from apex predators like leopards as these animals tend to live away from humans [53]. Access to anthropogenic food seems to be another driver of shelter and habitat selection in animals with coyotes choosing residential yards which afforded them this benefit [54]. Free-ranging dogs tend to prefer humans as food sources over foraging sites like dustbins and choose dens close to humans, sometimes within human homes,

elucidating the advantages of easy access of food resources and protection that the anthropogenic environment provides [52]. Black kites [55] in Delhi, India were found to settle closer to Muslim communities because of ritualised feeding practices, food subsidies, and human culture-driven dog elimination underscoring the influence of human culture and religion on the demography of these animals. The kites showed cognisance of functional relevance of urban configuration by selecting habitat spots at the intersection of high density of roads with intense human activity in neighbourhoods with poor waste management system to exploit refuse. Furthermore, the kites showed strategic and spatial awareness by building their nests within a radius of 1–2 km of multiple Muslim communities to spot and take advantage of conspecific cueing at multiple ritualised feeding spots to increase their foraging efficiency and volume and ultimately higher breeding output [55]. Additionally, birds living in human-built structures have been afforded higher breeding success. Barn owls were able to reduce their annual metabolic heat production by 19%, thus gaining thermal benefits and energy savings [56]. The ability to exploit humans for food and shelter is a behavioural adaptation that has helped these animals to survive in the urban landscape.

Human–animal interaction

As urban animals explore and engage with these novel anthropogenic resources, the chances of coming into contact with humans increases. Increasing rates of contact with people have been reported for various urban-adapted species like red foxes [57] and raccoons [58]. In fact, these close and frequent encounters with humans have made urban animals bolder and decreased their wariness to humans demonstrated by reduced flight initiation distances [59]. In the case of free-ranging dogs, the frequency of dog-human interaction is higher than conspecific interaction, elucidating the central role of humans in dog social network dynamics [60]. In fact, free-ranging dogs in Concepcion, Chile were able to observe, follow, and learn from pedestrians that crosswalks were the safest areas to cross a road and behaved as if they were affiliated with the residents [61]. As a result of their close and frequent interactions with humans since birth, free-ranging dogs can understand certain human-generated cues without being formally trained for it. For example, they are sensitive to human attentional state and show the capability to understand human intentions and adjust their behaviour accordingly [62,63]. In fact, while these dogs are wary of unfamiliar humans at first, providing them with a social reward (e.g. petting) over repeated interactions, thus displaying positive intention on the part of the human, makes them respond quickly and become more sociable as opposed to giving a food reward [64]. Free-ranging dogs not only show the capability of following complex pointing gestures, but adult dogs can adjust their behaviour in the presence of an unreliable pointer demonstrating behavioural plasticity in their interaction with humans [65,66]. As humans are a source of food and shelter for these dogs, understanding anthropogenic cues and adjusting their behaviour accordingly is of value to these animals although it is important to note that it is the dogs' millennia long history with humans that has resulted in such high socio-cognitive abilities as compared to other urban-dwelling animals.

But increased contact with humans also results in increased human-animal conflict. For example, in India, wild elephants often raid villages and destroy crops. In August 2021, Union minister for environment, forest and climate reported the loss of 1401 human and 301 elephant lives in India from 2018 to 2020. Carnivores like coyotes and black bears have been known to attack people across USA [67]. In India, the dog-human conflict is a very pressing issue and most people have a negative attitude towards these dogs [68,69]. Often times, the cognitive abilities like neophilia and boldness that make urban-dwelling animals so successful in human-dominated landscape turn out to be the cause of conflict with humans. In a real-life case of curiosity killed the cat, New Zealand's endemic parrot, the kea which is characterised by object neophilia and play behaviour are killed by humans because of their habit of interacting and manipulating objects like car doors and dustbins [70]. Thus, it is imperative for urban animals to recognise, assess, and respond to the threat posed by humans and human-generated disturbances. For example, temporary anthropogenic disturbances like festivals which cause sudden overcrowding caused a shift in free-ranging dogs' [71] and European hedgehogs' [72] behavioural activity and avoidance of the core disturbance zone to avoid potential conflict and competition. Although, avoidance of humans seems to be the primary tactic adopted by most animals, sometimes, these conflicts and human-animal interactions in novel ways provide a background that brings the exceptional adaptability and cognitive skills of these animals to the fore. The baboon population of Cape Peninsula, SA, known for their raiding behaviour in urban spaces were found to be cognisant of lacunae in management strategy execution. The baboons were sensitive to inter-individual differences in ranger-management strategies in certain areas (e.g. vineyards) and exploited the differences between rangers. Thus baboons assessed the differential risk level of an area, sampled and integrated interspecific public information (activities of the rangers) and formulated their own strategies to make the most of available resources, a testament to the ingenuity of these animals. [73].

Humans are unique predators in the sense that the threat posed by them to animals around them is

differential in nature. Thus, animals need to be able to distinguish between dangerous and nondangerous humans. Indeed urban birds like pigeons [74] and mockingbirds [75] quickly learn to assess the threat posed by different humans, distinguish between neutral and hostile humans and respond accordingly. Furthermore, crows [76], magpies [77], and reptiles like skinks [78] are sensitive to the direction of human attention and a direct gaze is taken to be an indicator of higher predation risk causing the animals to initiate escape responses. Apart from direct gaze, irregular behaviour is another cue to risk perception. Grey squirrels were observed to be more reactive to pedestrians who walked off the beaten path, that is moved from footpaths to grassy patches which is generally not frequented by them [79]. Similar responses are given by marmots [80] and robins [81] to hikers and humans respectively who leave expected paths. An interesting example of behavioural adaptation to human disturbance comes from vervet monkeys in Lake Nabugabo, Uganda. The areas that the monkeys lived in and foraged were highly modified for agriculture. The monkeys had frequent interactions with humans and associated animals like dogs, both of which were a source of danger to the monkeys. The male monkeys were observed to display sentinel behaviour, a relatively unique antipredator behaviour for a primate. Males would often take a prominent position, high up on a tree, scan for approaching danger, and give alarm calls on spotting humans or dogs. Such unique behavioural adaptations are suggested to reduce human-related mortalities in these animals [29]. Recognising humans who may ignore, persecute, or help them is an important cognitive skill that may help animals to exploit anthropogenic resources. Such fine-tuned discriminatory abilities are displayed by crows who are able to distinguish between and remember dangerous and neutral faces after a brief encounter. This demonstrates heterospecific feature discrimination and long-term memory retention in these birds [82]. Additionally, American crows in rural areas are more wary of a human carrying a shotgun than just a human or one carrying a broom displaying object association and identification [83].

Discussion

Free-ranging urban animals display a wide variety of cognitive abilities. Despite facing multiple adversities, these animals are able to adapt to these novel challenges. Urbanisation is one such challenge that has far-reaching effects on the life history of these animals. In the coming years, more and more of the natural environment is going to make way for urban centres and instead of avoiding urban habitats, animals would have to find ways to adapt themselves if they are to survive. Instead of seeing this as a hindrance, urban environments are being recognised for the potential of biodiversity they possess. We must further investigate the opportunities provided by such an environment and seek to understand and quantify the width of cognitive and behavioural repertoire of urban animals that live within it. Below, we outline various ways in which studies on free-ranging animals in urban areas can be carried out and improved upon while keeping in mind the welfare of the animals that are starting to share space with us.

First, we need to consider animals as 'partners-in-science' instead of just subjects of our curiosity. While research with captive animals make practical sense and might even be necessary to answer certain questions, we must take into account the ethical considerations too. Our current knowledge about the psychological and sociological needs of animals behoves us to adopt ethically and scientifically progressive research paradigms that lessens the negative effects on the animals as much as possible. One of the ways is to test animals in their natural environment. Although research on animals in their natural habitat is on the rise, the number of such studies is relatively low. The inability to control various factors that would introduce a bias and limited sample sizes are some of the concerns for the scarcity [84]. But the rise in technological developments can bridge that gap. Technology would not only let us access more species, but devices such as accelerometers and geolocators give us information on movement rate, environmental information such as light and temperature, and even include cameras that can show us the behaviour of animals. Automation is already a critical part of comparative cognition experiments in captivity [85] and can be modified and extended to carry out experiments in natural settings. A few studies in semi-natural conditions have already used automation to successful effect [86,87]. Since urban animals are habituated to humans and human-made structures, we suggest that automation combined with voluntary participation on the part of the animals is the way to go forward while carrying out experiments on free-ranging animals. Studies on cetaceans [88], vervets [89], and free-ranging dogs [62,90] demonstrate the effectiveness of the voluntary approach. It must be acknowledged that, despite this habituation, not all species will show high levels of responsiveness to testing. The identification of species that are responsive to testing in the wild and the types of tasks that can be successfully and robustly conducted in the field will be a good starting point. As researchers, we need to design methodologies that can integrate both of these components while maintaining similar levels of rigour as captive experiments and improving on their welfare.

Second, research on urban wildlife ecology has so far been concentrated in North America, Europe and Australia and the Global South is under-represented [91]. Research shows that various factors like economics, politics and inequality lead to a lack of urban cognition and ultimately, urban ecology research in these countries

[92]. This is an oversight that needs to be rectified. The countries of Global South have some of the most unique and biodiverse species. More importantly, the countries of Global South are going through various stages of urbanisation. This provides a unique opportunity for research in that we can study the intersection of colonisation and urbanisation at the various strata of development. It is worth examining the differential nature of urban environments and the associated pressures that shape the life experiences and personalities of these animals and would provide us with valuable information about their situational responses during human-animal interactions [93]. Indeed, it has been suggested that the study of environmental predictability in both time and space and the ways animal deal with it is a knowledge gap that needs to be addressed [94]. Furthermore, this heterogeneity allows us the possibility of exploring the four stages of colonisation: arrival, establishment, increase, and spread- and the behavioural and cognitive adjustments that go with them. Thus, we suggest that Asian, African, and Latin American countries possess huge untapped potential for cognitive science and requires the focus and funding of the scientific community to fill the critical knowledge gap.

Third, research in behavioural sciences and animal cognition in general has always been limited to a few taxa and even in recent times it is skewed towards mammals and birds [95]. Reptiles and arthropods remain some of the least studied taxa in behavioural sciences and wildlife ecology [10,91,96]. This is detrimental to the development of cognitive science as only by examining the abilities of a wide variety of taxa and animals can we have a true understanding of the cognitive mechanisms, their homologies and analogies, and their evolution. For example, reptiles develop normally at a range of fluctuating temperature, unlike the stable development of birds and mammals. This accords us the opportunity to study the effect of differing environments in the early stage of life history on the cognitive abilities of individuals [97]. Future research should focus on under-represented animals to gain a fuller understanding of the evolution of cognitive mechanisms and compare species of interest in terms of phylogeny. Research could also look into the physiological changes accompanying these modifications and their role in aiding or hampering an animal's cognition and survival.

Fourth, as animals become integral part of the urban environment, we need to adopt approaches that fulfils the potential of human-made green spaces like vacant lots, residential yards, and business parks within the built-up areas of cities, and creates new habitat opportunities [98]. Conservation efforts have so far focussed on areas outside of urban boundaries and away from human-exploited lands (farms, for example), missing out on the conservation potential of the urban landscape. Understanding the factors that help humans and animals coexist together is important and wildlife conservation has to be directly integrated into the urban planning and design process. This will require close collaboration between ecologists, built environment professionals, and architects. Not only specialised professionals but the public themselves need to be involved in this process. To start with, greater effort needs to be expended to include people in the decision-making processes and scientific studies. A continued focus on engaging and educating the public, from the grassroots level, about urban animals can help mitigate the problematic interactions between humans and animals. We need to stop thinking about urban infrastructure from the rigid anthropocentric, human-only, point of view and perceive them as cohabitation opportunities for humans and animals. In the model 'wildlife inclusive urban centres', buildings are regarded as rocks or cliff-like structures for birds and porosity and spaces for nests were integrated into the structure [99]. These wildlife inclusive urban designs have proven to have economic advantages in the form of reduced maintenance costs. Thus, instead of viewing these urban animals as pests, we need to make our cities more sustainable to the animals who are forced to share resources with us. Management, and not extermination, should be the watchword here.

Conclusion

One of the most noted biologists of our time, E. O. Wilson, whom we lost recently, is known to have said, "The one process now going on that will take millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly our descendants are least likely to forgive us." With the growing pace of urbanisation, urban cognitive and behavioural ecology will gain greater pertinence in the coming years. More interdisciplinary and diverse research within the field will help fill some critical knowledge gaps. Understanding the mechanisms that animals use to survive in highly human-disturbed landscapes can aid in the designing of management plans and policy. As both humans and scientists, we need to view these animals as equal stakeholders while conducting research and designing future urban centres. Cognition in the wild, especially of urban-adapted species, is thus a theme for future research that will enable our cities to nurture more forms of life on land, as envisaged by the UN Sustainable Goals 11 (sustainable cities and communities) and 15 (life on land). It is our hope that more research will be carried out on the cognitive capabilities of urban animals, exploring the ontogenetic, genetic and evolutionary trajectories of their adaptations to the new 'wild' — the urban jungle.

CRediT authorship contribution statement

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Conflict of interest statement

Nothing declared.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest.

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This review examines the various cues used by wild animals during human–wildlife encounters to modulate their behavioural responses towards humans, the processing of information received, and the cognitive underpinnings of it all. It also examines how human interactions select for certain cognitive capabilities in animals to ensure higher survival thus having an impact on species population itself. This review tries to summarise the work done on the various cognitive and behavioural skills displayed by nontrained, nonhuman socialised wild animals.

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