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Wildlife Affordances of Urban Infrastructure: A Framework to Understand Human-Wildlife Space Use

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Landscape affordances, what the environment offers an animal, are inherently species-specific to the extent that each taxon has unique needs and responses to landscape characteristics. Wildlife responses to landscape features range on a continuum from avoidance to attraction and quantifying these habits are the backbone of wildlife movement ecology. In anthropogenically modified landscapes, many taxa do not occupy areas heavily influenced by humans, while some species seem to flourish, such as coyotes (*Canis latrans*) and pigeons (*Columba livia*). Sufficient overlap in landscapes designed for human purposes (e.g., freeway underpasses, channelized waterways, and cemeteries) but which are also suitable for wildlife (e.g., by providing sources of food, shelter, and refuge) underlies wildlife persistence in urban areas and is increasingly important in the world's largest metropoles. Studying these overlapping worlds of humans and wildlife in cities provides a rich foundation for broadening human perceptions of cities as ecosystems that exhibit *emergent hybridity*, whereby certain anthropogenic features of urban landscapes can be used by wildlife even as they maintain their utility for humans. By examining scaling dynamics of the *infrastructural signature*, the phenomena of urban wildlife movement patterns conforming to the shapes of human infrastructural forms, we hope to expand on prior research in wildlife landscape ecology by stressing the importance of understanding the overlapping worlds of humans and wildlife. Further knowledge of the *urban ecological commons* is necessary to better design cities where emergent hybridity is leveraged toward the management goals of reducing human wildlife conflict and promoting biodiversity.

Keywords: urban ecology, affordance, infrastructure, wildlife management, infrastructural signature, emergent hybridity, urban biodiversity, urban ecological commons

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INTRODUCTION: AFFORDANCE AND EMERGENT HYBRIDITY

As cities grow in size, novel ecologies develop where wildlife exploit the human habits, forms and land cover types that are prevalent and intense in cities, while other wildlife previously native to these areas are filtered out by similar patterns of urbanization (Cooper et al., 2021). Keeping in mind both the possibility of attraction and avoidance for specific species to urbanizing areas, we

suggest that one key to understanding wildlife persistence in the urban environment is to focus on the density and scaling of urban infrastructure. "Hard" infrastructural forms like electrical wires, roads, water pipes and dams have long been classical subjects of anthropologists because they play important roles in mediating human social behavior (Anand et al., 2018). They are the physical components of the systems that enable, sustain and enhance possibilities for humans–connecting people with resources and people with each other. While wildlife are known to exploit these structures as well, for uses that include hunting, movement corridors and breeding sites (Way and Eatough, 2006; Kalcounis-Rueppell et al., 2007; Reynolds et al., 2019), rarely are these forms seen from the perspective of wildlife management as loci of a multispecies co-existence. As centuries-long infrastructural projects begin to deteriorate in unexpected ways and the promises and potential perils of "green infrastructure" further come into focus (Tzoulas et al., 2007; Soulsbury and White, 2015), we believe attending to the ways wildlife are interacting with human infrastructural forms will invite more intentional, aware and proactive policy decisions regarding the relationship between city design and urban biodiversity, the management of human-wildlife conflict, and the possibility of complex and novel ecologies emerging as cities expand.

Many cities around the world (e.g., London, United Kingdom, Singapore, San Juan, and Puerto Rico) have been the subject of studies on urban wildlife across a wide range of taxa (Schilthuizen, 2018). Ranging from mosquitos flourishing in the tunnels of the underground metro to novel assemblages of predator and prey species forming in response to the forces of conurbation and globalization, cities offer the opportunity to attend to the details of these newly emerging ecologies (Tyler et al., 2016). Understanding the way cities might or might not provide good habitat for wildlife is a matter of learning what the urban environment affords different species and individuals. *Affordance* is a concept coined by the psychologist and theorist of visual perception James J. Gibson, and it refers to what an environment offers an individual, what it furnishes or provides, whether for good or ill (Gibson, 1986). According to Gibson, this term suggests a kind of complementarity between the animal and the environment such that a city might be thought of as a composition of many cities: coyote (*Canis latrans*) city, rat (*Rattus* spp.) city, cat (*Felis catus*) city, pigeon (*Columba livia*) city, and human city, etc. It is a way of marrying an animal to its environment by extending our conceptual reach as ecologists beyond the individual species' *umwelt* (von Uexküll, 2010) and toward something that is simultaneously a matter of perception but also a property of the physical world (Maturana-Romesin and Mpodozis, 2000). The ecological affordances of the city, then, are all the possible relationships between animals and their urban environments, whether these possibilities are now actualized or not (Norman, 1999).

The concept of affordance is useful to the urban ecologist for two reasons. Firstly, an affordance perspective frames wildlife management in cities as a process of understanding how some animals come to flourish in the urban substrate by learning how to navigate the human conventions of urban environments. "Affordances reflect the possible relationships among actors and objects: they are properties of the world," writes Norman (1999, p. 42). "Conventions, conversely, are arbitrary, artificial and learned. Once learned, they help us master the intricacies of daily life" (Norman 1999, p. 42). In these terms, the urban ecology is imagined as a multispecies user interface whose successful navigation is mediated by both resource availability and the behavioral flexibility (i.e., the capacity to learn behaviors appropriate for urban life) of animals transitioning from wildlands to urbanization. The city provides many opportunities, but how exactly wildlife learn to exploit the resources it may offer often remains largely unknown. Affordance frames the difference between the actual and the perceived wildlife affordances of the urban environment as a matter of sensory perception, and so highlights the role of signaling, communication, and information as important ecological drivers of urban wildlife adaptation. The city's intensely anthropological processes are not only energetic, they are also informational as well, or prone to convention in the terms of affordance, and they come to mean something to urban wildlife by way of those "differences which make a difference" in Gregory Bateson's formulation (Bateson, 2000). How does the urban red-tailed hawk (*Buteo jamaicensis*) come to interpret the tops of electrical poles as perches from which to hunt along the slopes of freeway interchanges? How does a cemetery come to stand for a good denning site to an urban coyote and how is this decision a factor of the coyote's understanding of which multispecies interactions might take place there? What cues might cause urban mountain lions (*Puma concolor*) to use one freeway overpass and not another to locate potential mates?

Secondly, by highlighting *all the possible* relationships between animals and the urban environment, an affordance perspective allows us to consider potential urban ecological arrangements which have yet to occur, but which either might prove useful for conservation purposes or possibly detrimental to urban quality of life. Examining the full suite of species-specific affordances of an area can provide insights into how cities can become urban arks for the preservation of endangered species threatened elsewhere (Shaffer, 2018). Additionally, it may be possible to alter the design of cities to diminish the perceived affordances for invasive or nuisance species in an effort to stem their spread (Belant, 1997). Affordance invokes the difference between the possible and the actual and highlights the role of perception in moving our experiences between the two. Leveraging a species-based affordance perspective can open the imagination to many possible futures of cities as more biodiverse ecosystems.

Since an environment might afford many things for different species and individuals, the concept of affordance also draws our attention to the ways in which specific features of the urban landscape are the common grounds for the overlapping worlds of different species. Different features of the urban landscape can come to mean different things to different animals, whether across the human-non-human divide or between any two wildlife species (**Figure 1**). A cemetery means something different to a human than to a coyote than to a kestrel (*Falco tinnunculus*). For humans it is a place of mourning, and an infrastructure that provides cultural meaning in the assurance of a safe resting place for the dead. For a coyote a cemetery is hunting ground or a place to find food left behind by humans, and also a site of refuge from

FIGURE 1 | Cityscapes contain different affordances for different species. While urban infrastructure is generally designed either for direct human use (sidewalks and office buildings) or indirect human use (channelized waterways and shade trees) these infrastructures also offer an array of other uses, both realized and potential, for non-human species. For example, ledges of buildings might become roosts for pigeons, trash cans provide food resources for many species, and channelized waterways serve as water sources, hunting grounds, and movement corridors that are out of the watchful eye of people for coyotes. The highlighted areas in each panel suggest possible affordances specific to each of three examples species' unique perceptual abilities and needs. Illustration by Rigel Stuhmiller.

the daily bustle of the city. And, for a kestrel it could be the site of the few remaining native oak trees in a city, and so an opportune place to find a tree cavity for nesting.

As cities increase in size, some features of the urban landscape, like infrastructures, come to increasingly exhibit hybrid functionality for both humans and wildlife as cultural and ecological processes begin to combine in unpredictable ways (Alberti, 2016). The co-location of roads linked with ports and light rail become the vectors of seed dispersal and facilitates the movement of invasive species (e.g., Wichmann et al., 2009). "In coupled human-natural systems, networks are not governed by either natural selection or human ingenuity alone. Emerging networks are hybrid and novel expressions, and their functions emerge from interactions among natural and social networks," writes Alberti (2016, p. 21) in her book *Cities That Think Like Planets*. Further, while structures like flood control channels, cemeteries or railways may be present in cities of a range of sizes and human densities, in the largest urban centers these spaces are generally larger, more interconnected and may provide an important respite from human activity when compared with the surrounding areas. These factors are likely to make these infrastructural spaces more attractive to a range of wildlife within urban environments. Thus, over time, novel interactions, processes, and behaviors may emerge (Lowry et al., 2013). Within human infrastructural networks, animals are finding such varied affordances as hunting grounds, thoroughfares of their own, nest sites, or simply just a refuge from human attention (see "geography of attention," below); while historically these hybrid spaces have been unintended and unplanned, taking into account affordances of urban landscapes can leverage urban infrastructure to support biodiversity.

In this light, the degree to which we can reasonably expect the natural world to continue undergirding our societies, to serve as the infrastructure of our infrastructure, so to speak, is also a matter of what the structures we build come to afford non-humans. In the Anthropocene, it's no longer feasible to theorize "nature" as separate from human design, as our choices have wrought an immense impact on natural systems at both the local and the planetary scale. This increasingly obvious entanglement of the natural and the cultural is why studying "emergent hybridity" as a novel phenomenon is a critical opportunity for urban ecologists, and one with substantive management implications for wildlife in urban areas and possibly beyond. Since urban structures are designed by humans and, as of now, are only accidentally places where a multiplicity of human and wildlife affordances come to exist simultaneously (sometimes synergistically and sometimes in conflict), a better understanding of "emergent hybridity" should offer insights into the improvisational arrangements already occurring and a window through which to imagine and realize the many future possibilities of green infrastructure as an urban ecological commons. Identifying opportunities to further foster emergent hybridity empowers urban planners to intentionally manage necessary infrastructure to enhance biodiversity.

Understanding wildlife persistence in urban areas often relies on the assumption that animals flourishing in the urban ecosystem are doing so because of their ability to create worlds for themselves apart from humans. For instance, urban habitat surveys tend to reduce the specificity of urban anthropological forms in the process of understanding urbanization's pernicious effects (Moll et al., 2019). Studies of "connectivity" often assume that dramatic human landscape changes diminish certain species ability to move around the city (Wade et al., 2015). An "island biogeography" approach usually posits urban animal habitat existing as small habitable islands in an otherwise uninhabitable sea of human modified landscapes (Johnson and Munshi-South, 2017). And a focus on the importance of urban greenspace as part of a land sparing conservation strategy does not usually differentiate between human footprint and human presence (Soga et al., 2014; Nickel et al., 2020). Unlike these approaches, our marriage of the concepts of "affordance" and "emergent hybridity" advances an understanding of the way wildlife might use human infrastructural spaces in cities by inclusively viewing the overlapping worlds of humans and non-humans together. By attending to this confluence, the success of a given species in highly urban areas becomes a question of these animals' ability to leverage needed resources from infrastructure largely intended for human use, whether intentionally designed as such or as the result of human accident and evolutionary pre-adaptation. By viewing cities with multiple and species-specific affordances in mind, we see that urban ecosystems are richer and more complex than we might have otherwise imagined.

THE INFRASTRUCTURAL SIGNATURE

Cities are arguably the world's most spatio-temporally dynamic ecosystems, and for wildlife living within anthropogenic systems, flourishing in the urban ecosystem is a matter of being close but not too close to humans moving through space and time. In order to persist, urban animals must learn the conventions of city rhythms.

Over the span of decades, urban growth can transform ecosystems and have evolutionary consequences for wildlife

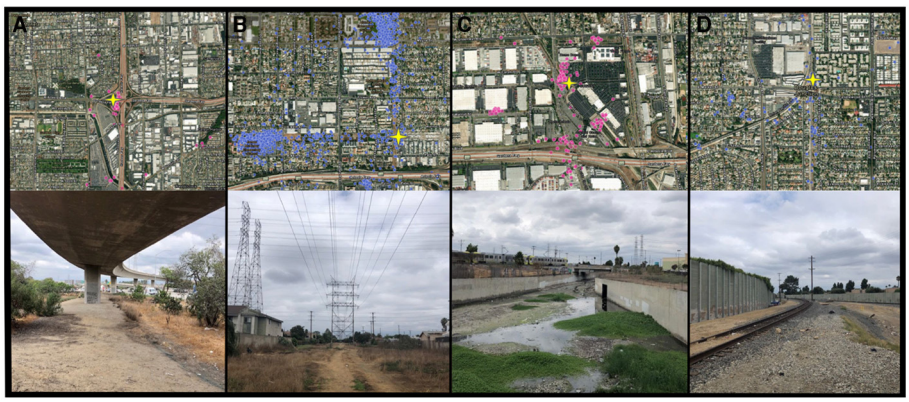

FIGURE 2 | The infrastructural signature in Los Angeles, California, as shown in coyote space use. The figure illustrates GPS location data showing how individual coyotes selectively use human infrastructural forms in South Los Angeles: **(A)** freeway interchange, **(B)** power line corridor, **(C)** flood control channel, and **(D)** railway lines. Image boxes on the top row show aerial maps with coyote GPS collar locations; photos on the bottom row offer an on-the-ground perspective from locations indicated by a yellow star on the corresponding aerial map. Base map powered using ArcGIS with software from Esri, with data points provided by Dr. Niamh Quinn, UCANR. Photographs by Chase A. Niesner.

(Johnson and Munshi-South, 2017; Schell et al., 2020b). Like all environments, cities have socio-ecological trajectories; city age, cultural history and former land uses all influence the ecological response to the urban environment (Ramalho and Hobbs, 2012; Schell et al., 2020a). Within the span of days, animal movement and habitat selection are influenced by fluxes in human presence and daily rhythms (Nickel et al., 2020). For instance, temporal patterns created by commuting and those relating to human leisure often result in animals adjusting their movement patterns to accommodate the intricate human processes of daily life (Nix et al., 2018). City streets or city parks might be unavailable during the day because of foot and auto traffic, but become prime habitat in the dead of night.

As much as urban wildlife might seek to avoid the wrong kind of human attention, human-wildlife interactions in cities are also sometimes defined by considerable ambiguity. From the perspective of a coyote, for instance, a human could be both an apex predator who might trap or kill them, a photographer who keeps their distance, or even a potential source of food or water. In fact, many municipal coyote management plans seek to address these uncertain terms specifically by encouraging residents to stop feeding coyotes and to haze them instead, thereby re-instilling a fear of humans (see Culver City Coyote Management Plan, 2021).

For animals like coyotes, that avoid most human contact but remain close enough to exploit the resources humans might offer, urban infrastructural spaces in particular afford the opportunity to live nearby but also to remain somewhat hidden. Many urban infrastructural forms are integral to the functioning of cites and the livelihoods of the people who use them, but are rarely visited by humans unless the function of the infrastructural space is broken and in need of repair or maintenance (e.g., neglected corridor used for power lines). And since these urban forms are the physical components of a networked society, infrastructures literally connect different parts of the city and thereby afford wildlife a range of options with which to simultaneously move around while remaining largely out of sight.

By way of proof of concept, we illustrate what appears to be an "infrastructural signature" to urban coyote movement in South Los Angeles, California, one of the densest and most urban areas in LA County. Here, urban coyote movements seemingly conform to the shapes of human infrastructural forms in highly urban territories (**Figure 2**). While coyote space use in wildlands remains relatively consistent in shape and size, highly urban coyote territories vary, shrinking into infrastructural spaces during the day and expanding into the broader urban landscape at night (Riley et al., 2003; Grubbs and Krausman, 2009; Thompson et al., 2021). Such emerging, dynamic, and hybrid human-wildlife spaces may be critical for wildlife persistence in these areas, and studying them is an opportunity to better understand the multispecies, urban ecological commons that sustains urban biodiversity and human society simultaneously.

Comparing coyote space use over a rural to urban gradient, it becomes clear that urban coyote movement patterns become more complex and more fragmented than coyote space use on the urban-wildland interface. For example, in a city of medium density with significant green space (e.g., Denver and Colorado) coyotes spend their days resting in natural areas and then venture out into the surrounding neighborhoods at night for food, water and other needs (Poessel et al., 2016). However, in the denser portions of a larger city like Los Angeles, where many coyotes are now living, coyotes appear to spend their days taking refuge in infrastructural spaces (rather than natural areas) and then similarly steal away into surrounding neighborhoods for sustenance at night. Even though these urban movement patterns exhibit more complexity and fragmentation than those in rural areas or at the urban-wildland interface, these urban infrastructural spaces are nonetheless miniature "micro-ecologies," with their own assemblage of actors, feedbacks, and suites of multispecies interactions; infrastructural spaces provide

both refuge and proximity to human resources that can be exploited by coyotes to subsist in such a dense urban area.

Different infrastructural forms might offer their own unique wildlife affordances: a freeway interchange is not the same as a flood control channel, they are distinct "micro-ecologies." And yet, some affordances of infrastructural forms might be generalizable across the entire category. What might human infrastructure generally afford urban wildlife, like coyotes?

Firstly, coyotes in cities must largely avoid human detection if they are to survive. And, in what we're calling a "geography of attention," infrastructural spaces, though intensely modified by humans, offer some respite from human presence because most people rarely visit or spend large amounts of time there. Further, these spaces are often fenced off from the public for safety reasons. With the goal of better understanding the ecological role of these interstitial spaces, we consider geographies of attention to be similar to "landscapes of fear," which describe the spatial variation in the non-human perception of risk and their responses (Laundré et al., 2001; Bleicher, 2017; Gaynor et al., 2019). By emphasizing "attention" rather than "fear," we underscore the fact that urban wildlife are constantly interpreting human behavior and deciding for themselves whether an individual human is dangerous or not. The "geography of attention" is intended to highlight the complications arising from these more ambiguous human-non-human relations that arise in cities because of what living close to humans potentially affords wildlife: for better or for worse, not all humans are feared by coyotes, as some humans (and their commensals) have proven to be the locus of substantial resources (Hulme-Beaman et al., 2016; Larson et al., 2020).

Secondly, these spaces themselves often afford significant opportunities beyond refuge. For example, flood control channels provide a steady stream of water from local runoff in addition to connectivity with locations in the surrounding area. Cemeteries might provide a hunting ground or even the opportunity to be fed by humans who sometimes leave offerings at the graves of their deceased loved ones. And, around Los Angeles, in the cleared land under power lines often sit miles of plant nurseries, which grow a variety of fruiting trees and other shrubs that might attract coyotes and coyote prey species (Niesner, 2021, author's observations).

Finally, the infrastructural space affords the temporal flexibility that is necessary for coyotes to successfully navigate the aforementioned risks and rewards surrounding the rhythms of urban life. Though further analysis must be undertaken, it's likely that the infrastructural signature itself calcifies during the day and then loosens at night when the city writ large becomes more hospitable to urban wildlife for a variety of reasons. These spaces provide refuge and a point of departure for forays into the wider urban substrate. Although the "infrastructural signature" as described here takes inspiration from fieldwork and observations concerning urban coyotes, we believe the dynamics described apply to other taxa as well, currently and in the future.

Cityscapes may present qualitatively different opportunities for generalist compared to specialist species; for instance, generalist species like coyotes and racoons might be more likely to exploit wholly novel urban ecosystems that were unfamiliar to their ancestors, whereas specialist species like mountain lions or kestrels might be more likely to exploit remnant habitat within urban ecosystems that are similar to wildlands familiar to their ancestors. Since generalists and specialists can impact ecosystems rather differently, and themselves are impacted differently by changing ecological conditions, any environmental stewardship of urban areas must be taken with great care and consideration of the urban ecosystem as a complex whole.

In future work on the infrastructural signature, we recommend beginning with individual species by asking what affordances they're able to register by way of their species-specific umwelt. Then, *via* analyses of movement sequences or camera trap data it will be possible to determine whether a species' space use patterns indeed conform to human infrastructural forms. This two-step process is what distinguishes an affordance-based management approach from other management strategies, in that it combines a cognitive understanding of a given species sensorium with a focus on the affordances of the urban environment offered by specific urban infrastructural forms.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The phenomena of "emergent hybridity," and more specifically the possible infrastructural signature of urban animal movement patterns, likely only emerges in cities of a particularly large size and human density. In cities of grand scales, there is more intense human presence and less wildland space; the necessities of navigating the "geography of attention" mean that animals will come to find infrastructural spaces useful for their purposes of remaining hidden while also close to needed resources. In these highly urban contexts, human-designed infrastructures may become more desirable as habitat over time and across space, leading to the particularly emergent quality of infrastructural hybridity.

Historically, large cities have also hosted a greater expanse of built areas, and due to long standing social policy in the United States, many American cities like Los Angeles are still experiencing the ongoing legacies of segregation along race and class lines. The resulting unequal distribution of a range of resources, ecosystem services and biodiversity included, is still a present-day structural reality whose lingering effects must be understood as both a social and an ecological force (Schell et al., 2020a). We believe further inquiry into the possible emergent hybridity of urban infrastructure is one such way to understand the social and ecological together, as it draws our attention to the present and ongoing novel ecological arrangements already occurring in urban spaces long ignored by wildlife biologists and conservationists alike. As cities attempt to address inequality and create the green infrastructure of the future, policy makers must contend with the fact that large infrastructural projects have historically contributed to the problem of segregation and displacement (and may do so again if care is not taken), while also recognizing the present and possible future ecological potentials of infrastructural hybridity.

The degree to which humans might welcome the presence of wildlife in cities varies drastically across taxa and also across contexts; in many cases the future of specific human-wildlife interactions in cities is still wildly contingent. For instance, though most people would likely welcome a peregrine falcon nesting pair on the window-ledge of a skyscraper, the presence of urban coyotes is an intensely rancorous and politically divisive topic in many urban areas across the country (Green, 2019). By attuning ourselves to the wildlife affordances of urban infrastructure, we'll soon better understand the processes by which cities attract some species and not others, and so also be guided to the mechanisms by which to manage the very human habits undergirding both positive and negative human-wildlife interactions. Though the question of how wildlife are flourishing in cities is a matter of understanding wildlife affordances, the question of how humans and wildlife might live together is a matter of the confluence of wildlife and human affordances, or what each might offer the other's quality of life, and so perhaps a question better suited for anthropologists and ecologists working together.

Once one begins to think about these ideas, and to think how the importance of urban infrastructure might vary with city size, a number of testable hypotheses and questions arise. For instance, what, precisely, is it about city size (area, density, population) that drives scaling patterns in affordances and is it the same for different species? Do we want to design urban ecological affordances for all animals or only some animals? How should we recognize the inherent unpredictability of the urban ecology, the accidents, changes and contingencies which are inevitable? Do different urban infrastructures afford specific ecological relations that attract and repel specific species? How exactly might these "micro-ecologies" be related to one another but also to the wider city? How can we leverage ecological affordances to reduce human wildlife conflict, repel pest species, and protect vulnerable species and ecological processes in urban environments? Will human residents of cities welcome relations with some wild fauna but not others, and if so, how might community co-existence education be a critical component of these urban ecosystems? What are the evolutionary consequences of emergent hybridity? Does the infrastructural signature apply to all animals? How does affordance-based management allow us to better understand the different ways both generalists and specialists might adapt to cities or be filtered out of the urban ecology? Which traits enable adoption of the infrastructural signature? Does the strength of temporal patterns of infrastructure use vary as a function of city size? These are but a few of the questions stimulated by adopting a perspective that seeks to identify affordances and emergent hybridity. All are ripe for testing.

A better understanding of how human-designed features in the urban landscape are also shared habitat for wildlife will likely lead to improved wildlife management in these areas, and hopefully to increased access to biodiversity for marginalized groups as well. We expect strong scaling effects on the importance of urban infrastructure whereby as cities become larger and more urban, human features will play an increasingly important role in defining biodiversity. Indeed, we expect supranormal scaling relationships (Uchida et al., 2021) and this has important implications for defining wildlife management in increasingly large cities.

While different species will inevitably come to discover the various affordances of these infrastructural forms, whether we design for them or not, identifying how animals come to perceive and utilize these spaces will improve the ecological stewardship of these areas and lead to a better awareness of their role as shared habitat within the city. We hope attention to the hybridity of urban infrastructure invites further study of these discrete micro-ecologies of the city, and an opportunity to further encourage the successful coexistence of humans and biodiversity.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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