

Neophilia, innovation and learning in an urbanized world: a critical evaluation of mixed findings

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Conversion of natural environments to cities confronts animals with abundant novel opportunities. Research on perception of threat in urban animals is fast expanding, but analyses of their capacity to exploit novel resources are scant. Experimental predictions regarding urban/non-urban behavioral differences are grounded in disparate statements regarding the ecological conditions that prevail in urban environments. We evaluate critically whether urban habitats favor high neophilia, innovation and learning in established populations. Extreme spatial complexity of urban landscapes coupled with increased resource predictability due to human routine activities should favor neophilia and learning. Cities provide exciting new opportunities to investigate empirically whether variation in these traits is related to variation in environmental complexity and predictability as forecast by a body of theoretical work.

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Introduction

Colonization of novel environments presents wildlife with new ecological opportunities in response to which those animals adequately behaviorally equipped can thrive [1,2]. Three categories of behavior are thought to determine the capacity to adopt novel ecological opportunities: 1. the balance of attraction (*neophilia*) and avoidance (*neophobia*) of novelty, 2. the propensity to invent new behaviors or use pre-existing ones in novel circumstances (*innovativeness*), and 3. the capacity to learn [3]. Recently, Tebbich *et al.* [4] have described how encountering novel opportunities, interacting with them and learning about those interactions, form fundamental behavioral components of an integrated framework of

innovation, which are influenced by a variety of perceptual, motor and cognitive processes.

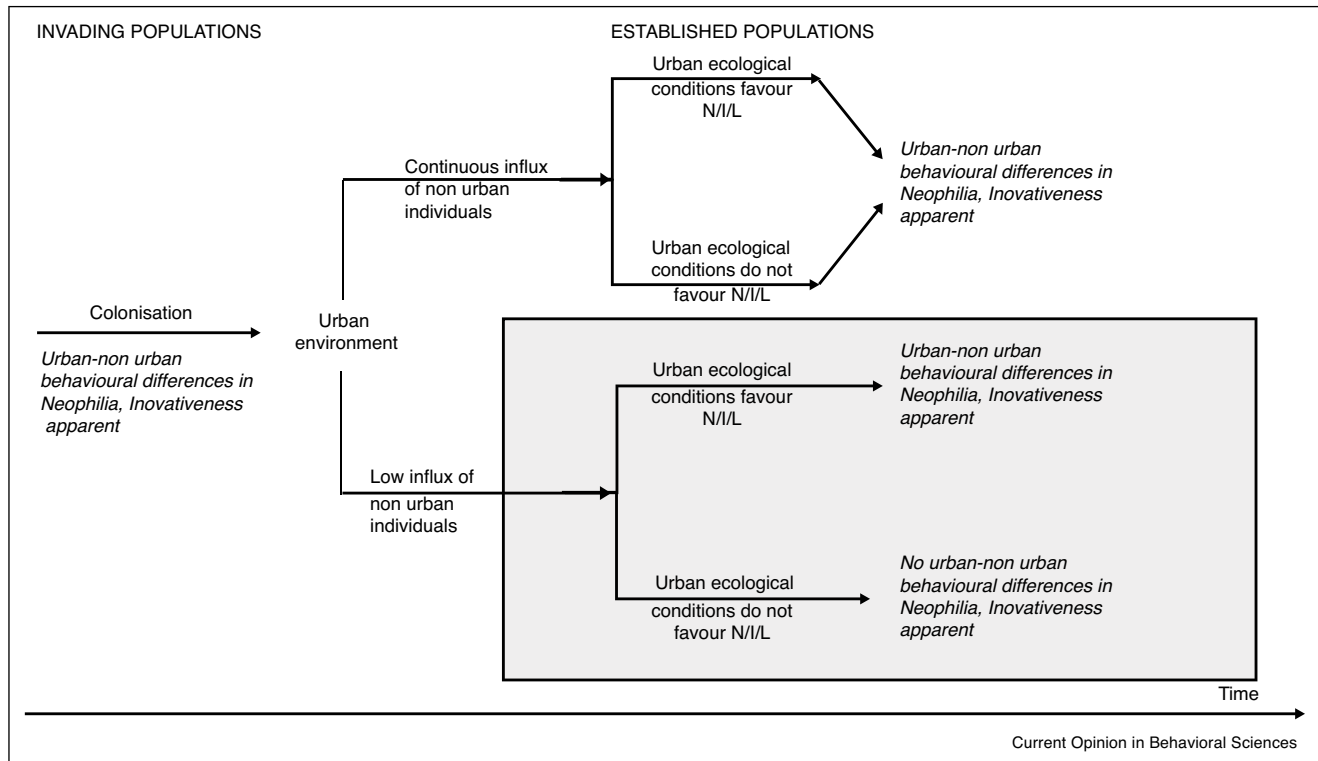
Urbanization is currently the fastest form of habitat transformation globally [5]. There is little doubt that sudden conversion of natural landscapes to man-made structures accompanied by an influx of humans confronts wildlife with countless novel threats [6–8]. But habitat conversion also creates a host of yet unexploited novel ecological opportunities [6–8]. It is perhaps surprising therefore that research on the effects of urbanization on wildlife to date has focused much more heavily on how animals cope with the former than how they take advantage of the latter. This is particularly surprising given that colonization of urban habitats is a form of biological invasion and capacity to adopt novel opportunities has attracted considerable research effort in invasion biology [2,9,10].

The invasion process can be broken down into a series of stages [11]. Behavior adaptive at the early stages (*e.g.*, colonization) might not be adaptive at later stages (*e.g.*, establishment) [12,13]. The first generations of urban colonizers might have an enhanced need to explore novelty, behaviorally innovate and learn [8] (Figure 1). Given the costs associated with interacting with, and learning about, novelty [14–16], however, these traits should only be maintained in generations of established populations if these populations are continuously supplemented by new non-urban colonizers, or if urban populations are isolated but ecological conditions are such that these traits continue to provide an adaptive advantage (Figure 1). This latter scenario is the focus of the present opinion piece.

In the behavioral literature comparing urban and non-urban wildlife, experimental predictions are often anchored in broad statements about prevailing urban ecological conditions. The result is an accumulation of seemingly contradictory statements. Some authors note that food is superabundant, but unpredictably distributed [17], while others state that resources tend to be more stable [18]. Others see urban environments as more complex and more unpredictable [19] or just more complex [20], while yet others flag their variability [21]. Some authors point to greater food availability including year-round food resources [7], whereas others test predictions that competition for resources is stronger [22], and threats more common [23].

The purpose of this opinion piece is to evaluate critically whether there are grounds to hypothesize that neophilia,

Figure 1



Schematic depicting the relationship between invasion stage and urban-non urban differences in behavior. Whether or not behavioral differences in neophilia (N), innovativeness (I) and learning (L) are apparent in comparisons of urban and non-urban birds will depend upon whether focal individuals have been collected from populations at an early stage or at a later stage of the invasion process. If focal birds originate from long-term established populations, the occurrence of urban-non urban differences will depend upon the extent to which those urban populations are isolated from non-urban influx, but also on the extent to which urban environments favor the evolution of these traits. Key urban ecological variables include environmental harshness, complexity and within-generation predictable variation (see text for more details). Most comparative studies so far have overlooked the complexity depicted in the diagram (but see Refs. [79,80]), which might help explain disparate findings. The shaded area highlights the scenario discussed in the present opinion piece.

innovation and learning should be generally adaptive in established urban populations and to identify more clearly why. We begin by briefly reviewing the comparative behavioral literature examining these traits in birds, the most intensely studied taxonomic group in the urban context [24]. This exercise highlights the extraordinary collection of discrepant findings. Then, we extract predictions from a body of mostly theoretical research describing the environmental parameters that drive the evolution of neophilia, innovation and learning, and examine which of these are most likely to characterize urban environments. It is not our intention to review either the theoretical or urban ecological literatures exhaustively, but merely to extract several key predictions and evaluate them against current urban ecological knowledge.

Current state of knowledge

Responses to novelty (Table 1)

Comparative analyses of responses to novelty of urban and non-urban birds have been undertaken multiple times. Some studies suggest greater neophobia and lower

neophilia in urban birds (Table 1), but this pattern is far from consistent. For example, shiny cowbirds are no more neophobic in urban than in non-urban areas [19] and urban house sparrows are more neophobic in some urban areas [19], but no different in others [25] (Table 1). Captive bred urban European blackbirds are less neophilic than rural blackbirds but only during summer [18]. Other studies have found the opposite patterns with city birds being less neophobic and more neophilic (Table 1).

Findings from multispecies comparisons are equally mixed. In some cases, urban birds are less neophobic [17] and more neophilic than non-urban birds [26]. In other cases, urban birds are less disturbed by humans, but not less neophobic [27] or decreases in neophobia are category-specific [23].

Innovation and learning

The few comparative analyses of innovation and learning have also revealed mixed patterns of findings. In some species, urban individuals solve novel foraging problems

Table 1

Summary of empirical studies comparing neophobia, innovativeness and learning in urban versus non urban birds under both wild and lab conditions

Behavior	Species	Trend	Experiment	Reference
Neophobia	House sparrow (<i>Passer domesticus</i>)	U > M	Wild	[19]
Neophobia	Eared dove (<i>Zenaidura macroura</i>)	U > M	Wild	[19]
Neophobia	Barbados bullfinch (<i>Loxigilla barbadensis</i>)	U > R	Lab	[30]
Neophobia	European blackbird (<i>Turdus merula</i>)	U > R	Lab (common garden)	[18]
Neophobia	Common mynas (<i>Acridotheres tristis</i>)	U < SU	Lab	[28]
Neophobia	12 species	U < R (category specific)	Wild	[23]
Neophobia ^a	Great tits (<i>Parus major</i>)	U < R	Wild	[17]
Neophobia ^a	18 bird species	U < R	Wild	[17]
Neophobia	5 species	U = R	Wild	[27]
Neophobia	House sparrow (<i>Passer domesticus</i>)	NS	Lab	[25]
Neophobia	Shiny cowbird (<i>Molothrus bonariensis</i>)	NS	Wild	[19]
Neophilia	European blackbird (<i>Turdus merula</i>)	U < R (seasonal)	Lab (common garden)	[18]
Neophilia (food)	43 species	U > R	Wild	[26]
Innovation	House sparrows	U > R (task and body size specific)	Lab	[81]
Innovation	Barbados bullfinch (<i>Loxigilla barbadensis</i>)	U > R	Lab	[30]
Innovation	House sparrow (<i>Passer domesticus</i>)	U > R	Lab	[82]
Innovation	Great tits (<i>Parus major</i>)	U > R	Wild	[83]
Innovation	Common mynas (<i>Acridotheres tristis</i>)	U > SU	Lab	[28]
Innovation	Common mynas (<i>Acridotheres tristis</i>)	U = R	Lab	A. S. Griffin, unpublished data
Innovation	29 species	NS	Literature	[20]
Innovation	39 pairs of species	U > R	Literature	[29]
Learning (discrimination)	Barbados bullfinch (<i>Loxigilla barbadensis</i>)	NS	Lab	[30]
Learning (reversal)	Barbados bullfinch (<i>Loxigilla barbadensis</i>)	NS	Lab	[30]
Learning (discrimination)	Common mynas (<i>Acridotheres tristis</i>)	U < R	Lab	[21]
Learning (habituation)	House sparrows	U > R	Lab	[31]

Neophobia is most typically measured experimentally as a difference between a latency to feed from a familiar food container in the presence versus absence of a novel object. Innovativeness includes both an experimental measure of innovativeness, namely innovative problem solving, and a literature-based measure, namely counts of foraging innovation anecdotes. NS: no significant difference; R: rural; M: marshland; W: wildland; SU: suburbia.

^a The terminology has been changed by the present authors from neophilia to neophobia as the study's methodology corresponds to that more generally used to measure neophobia (willingness to feed in the presence of a novel object).

(an experimental proxy of foraging innovativeness) more quickly than non-urban individuals, but in other species the effect is task-specific or dependent upon the non-urban comparison group (Table 1). For example, urban common mynas innovate faster than suburban mynas [28], but not rural ones (A.S. Griffin unpublished data). Using a large scale comparative approach, Møller [29] found that counts of foraging innovations were higher in urban-dwelling avian birds than non-urban-dwelling ones, but Kark *et al.* [20] found no such differences.

Urban Barbadian bullfinches are no faster to learn associatively than rural individuals [30], whereas urban common mynas learn more slowly [21]. In contrast, urban house sparrows habituate (a form of individual learning) faster to humans than rural individuals [31].

In light of this accumulation of discrepant findings, we attempt to identify the key ecological parameters thought to shape the evolution of novelty responses, innovativeness and learning, and then ask which ones are most likely to operate in urban environments most generally.

Ecological conditions that shape novelty responses, innovativeness and learning Environmental variability and/or complexity favor neophilia

Greenberg and Mettke-Hofmann [32] proposed that under conditions of high environmental variability and/or complexity, the benefits of approaching and interacting with novelty should be high and animals should tend to be neophilic. In contrast, high predation increases the risks of interacting with novelty and should hence favor neophobia [32]. Important to note, however, is that this two-factor model proposes that animals can be both neophilic and neophobic. This occurs in combined conditions of high environmental variability/complexity and high predation, in which case high neophilia ensures that exploration occurs once neophobia has habituated [32]. As attraction to novelty depends upon stored knowledge of a familiar background against which novelty is detected, evolution of neophilia should also favor the evolution of learning [3,33]. Experience-dependent object-specific changes in neophobia should exert additional selection in favor of learning.

Environmental harshness favors innovativeness in the feeding domain

To our knowledge there has been no theoretical modeling of the environmental drivers of innovativeness. The intuitive idea that the tendency to behaviorally innovate should be advantageous during the early phases of invasion when environments are novel has been tested multiple times and found much support [9,34,35]. In established populations, avian foraging innovations are associated with harsh climatic conditions and food scarcities. Indeed, foraging innovations are more common in winter than in summer, as well as in resident than migratory birds [36]. Collected along a north-south gradient of decreasing environmental harshness, captive-reared black-capped chickadees (*Poecile atricapillus*) from northern populations solve a novel foraging problem faster than southern birds [37].

Environmental predictability and complexity favor learning

Loose references to an adaptive advantage of learning under conditions of environmental variability are common. Theoretical modeling has long identified predictable environmental change as a more specific evolutionary driver of learning, however. Further, classic work by Stephens [38] has stressed the importance of differentiating between within-generation predictability, namely whether the environment today predicts the environment tomorrow, and between-generation predictability, that is, whether the environment experienced by one generation predicts the environment experienced by the next generation. Mathematical modeling indicates that within- or between-generational change can lead to evolution of learning, but beyond that, within-generation predictability is a much heavier evolutionary determinant of learning [38].

More recently, modeling by Dridi and Lehmann [39] has indicated that between-generation predictability is not necessary for learning to evolve. Coupled with within-generation predictability, environmental complexity, defined as the number of distinct stimuli an individual encounters in its lifetime, favors the evolution of learning. The effect of environmental complexity is due to the benefits of being able to store and forget a large number of stimulus-response associations as they are encountered across time [39].

Dunlap and Stephens [40**] have also challenged the ‘learning folk theorem’, which holds that changing environments favor learning, but stable, fixed environments favor hard-wired behavior. The authors demonstrate both theoretically and experimentally that environmental fixity has two components. Whereas the fixity of the most adaptive, ‘best’ action (*e.g.*, lay eggs on an orange scent) selects against learning, fixity of a predictive relationship between an environmental stimulus and the best action

(lay eggs on a scent not previously experienced with quinine) favors learning. Learning is counter-selected only under conditions where the best action is fixed *and* the relationship between experience and the best action is unpredictable. The authors conclude that randomness of the experience-best action relationship, not fixity of the optimal action, is the most powerful selection force against learning. Overall, environments that change predictably within an individual’s lifetime, particularly coupled with environmental complexity, favor evolution of learning.

Prevailing ecological conditions in urban environments

Are urban environments harsher?

Temperate cities are characterized by low day-night temperature differences due to the absorption of heat during the day and re-release during the night. Cities have been found to be at times up to 10°C warmer than surrounding rural areas [41]. The same mechanism can buffer against cold winters and extend growing seasons.

At urbanization levels that include managed green spaces (*e.g.*, parks, gardens), local productivity is often higher than in surrounding wildland [42,43] and less seasonally and annually variable [44]. High productivity provides not only more plant-based foods, but also more (albeit taxonomically less diverse) invertebrate herbivores, in cities relative to *wildlands* [45,46**]. In contrast, urban habitats often have lower abundances (and diversities) of many plant-dwelling invertebrates relative to *rural areas*, not through lower primary productivity, but as a consequence of more top-down control by high densities of a few highly effective avian predators [44,46**].

Overabundant anthropogenic food sources might compensate for loss of invertebrates [47–50]. Human discards tend to be rich in lipids and carbohydrate, however [51,52]. Hence, although food is likely to be more abundant, specific nutrients (*e.g.*, protein) are probably more scarce [53,54*,55]. Overall, urban habitats appear to be less, rather than more, harsh than non urban environments.

Are urban foods more predictable (Box 1)?

Food is generally thought to be more predictable inside cities [49]. Urban predictable anthropogenic food sources (PAFS) include bird feeders and food dumps [56]. Human discards around fast food outlets, supermarkets and school playgrounds on the ground and in dustbins are also likely to be more predictable in space and time, particularly for those species capable of learning to use humans as a cues for food availability [57]. There is increasing evidence that many urban birds respond to human behavior, including cyclical routine activities such as weekly schedules [58–61].

Box 1 Complexity and predictability of urban ecosystems.

At global scales urban environments become more homogenous than natural environments. At lower scales of resolution, urban landscapes are formed by a mosaic collection of impervious surfaces (*e.g.*, buildings), green spaces (*e.g.*, sporting grounds and gardens) and blue spaces (*e.g.*, ponds) [77]. The integration of built and non-built structures yields complex and spatially heterogeneous urban configurations [73**,74]. Theory predicts that environmental complexity should favor the evolution of neophilia, as well as learning as long as environmental variation is predictable. This leads us to consider what is known about the predictability of urban environments.

Urban environments can no doubt vary in predictability in many regards (*e.g.*, food availability, nesting opportunities, predation), all of which might affect individual behavior differentially. Food is a core ecological factor regulating population growth through bottom-up control [49]. It seems therefore reasonable to ask more specifically whether food is more predictable in urban habitats. Urban (most often exotic) plant diversity is highly unpredictable in space. Indeed, in some cases, spatial auto-correlation in plant diversity is practically in-existent above the scale of the house plot, and within plots, plant species richness can vary by an order of magnitude [72]. On the other hand, urban vegetation is temporally more predictable than some seasonal natural resources as human behavior shields it from climatic impacts (*e.g.*, lack of water; low temperatures) [49,73**]. In addition, human activities increase the predictability of other key urban foods. These include bird feeders and human refuse, both of which are linked to human activities and schedules and can therefore be predicted readily on the basis of human behavior [57,60,78].

Specific analytical tools exist for quantifying to what extent current ecological conditions predict future conditions (reviewed by Ref. [79**]). Methods for measuring predictability of quantitative temporal variables include correlograms, spectral analysis and wavelet analysis. Those for measuring predictability in spatial variables include spatial auto-correlation statistics. Alternative methods can be applied to discrete environmental variables (*e.g.*, presence/absence of a predator). Any measurement of environmental complexity and predictability should be undertaken at spatial and temporal scales relevant to the biology of the organism of interest. A good starting point would be to consider the scale at which the species moves through the urban matrix in search of mates, food, territories, shelter and conspecifics. In addition, these tools can be used to assess the scale at which the environment is predictable and beyond which it is no longer predictable. By relating this scale to that most relevant to an organism of interest, one can determine whether the individual experiences the environment as predictable or not. For example, if an environmental variable is spatially predictable at a scale equivalent to the size of a bird's territory, then a territorial individual is likely to experience the environment as predictable but a vagrant individual which travels through multiple territories is likely to experience it as unpredictable.

Is predation lower in urban environments?

Whether predation is higher or lower in urban areas compared with non-urban areas is contentious [62]. There is evidence for both lower and higher predator densities [46**], but densities might not reflect predation risk accurately [63]. Studies measuring predation rates on artificial nests also diverge in their findings [64,65]. However, there is an increasing awareness that cats pose one of the two greatest threats to urban birds along side window panes [66–69]. Predation levels remain influenced by a

large variety of landscape features, such as vegetation structure [70,71], as well as species-specific reproductive behaviors, including nest height [70].

Are urban habitats more complex (Box 1)?

Urban landscapes are characterized by extremely high spatial heterogeneity both in terms of resource levels and habitat structure [44]. In some instances, human activities have practically eliminated spatial auto-correlation in plant diversity above the house plot, and within plots, plant species richness can vary by an order of magnitude [72]. The integration of built and non-built structures yields complex urban configurations [73**,74].

Conclusions

Despite widespread suggestions that species' urbanization should be associated with increased behavioral flexibility, so far, research on three of its key components, namely neophilia, innovativeness and learning, has found no clear patterns of differences among urban and non-urban birds. We suggest that lack of attention to a species' invasion stage and lack of clear ecologically grounded predictions are impediments to understanding this body of mixed findings. Current ecological research suggests that urban environments are less, rather than more, harsh in terms of climate and food abundance, reducing the need for foraging innovations in established urban birds. In contrast, urban environments are spatially highly complex and foods tend to be more, rather than less, predictable, pointing to an increased need for neophilia (to deal with complexity) and learning (to take advantage of predictable variation). Predation levels vary tremendously along a complex set of ecological dimensions, suggesting high neophilia should be coupled with developmentally plastic levels of neophobia which will therefore vary according to local predation risk [3].

There exist quantitative methods for measuring environmental predictability both in time and space, which need to be applied at spatial and temporal scales relevant to the biology of the species of interest (Box 1). Rather than urban versus non-urban (*e.g.*, rural) comparisons, we suggest behavioral comparisons of birds living within different types of urban habitats (*e.g.*, different cities with distinct landscape profiles) will be more fruitful [28] and inform urban design more directly.

Future research should bear in mind that urban pollution and nutritionally deficient food sources, particularly during chick development, might impact cognitive abilities negatively, including novelty responses and learning [33,75]. In addition, urban environments are themselves changing, with green areas shrinking and asphalt expanding [76]. Clearly, we are a long way from understanding how urban environments affect avian behavior, but working alongside urban ecologists to develop solid hypotheses will be key.

Conflict of interest statement

Nothing declared.

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