

Which Traits Influence Bird Survival in the City? A review

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Abstract: Urbanization poses a major threat to biodiversity worldwide. We focused on birds as a well-studied taxon of interest, in order to review literature on traits that influence responses to urbanization. We review 226 papers that were published between 1979 and 2020, and aggregate information on five major groups of traits that have been widely studied: ecological traits, life history, physiology, behavior and genetic traits. Some robust findings on trait changes in individual species as well as bird communities emerge. A lack of specific food and shelter resources has led to the urban bird community being dominated by generalist species, while specialist species show decline. Urbanized birds differ in the behavioral traits, showing an increase in song frequency and amplitude, and bolder behavior, as compared to rural populations of the same species. Differential food resources and predatory pressure results in changes in life history traits, including prolonged breeding duration, and increases in clutch and brood size to compensate for lower survival. Other species-specific changes include changes in hormonal state, body state, and genetic differences from rural populations. We identify gaps in research, with a paucity of studies in tropical cities and a need for greater examination of traits that influence persistence and success in native vs. introduced populations.

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1. Introduction

Today, urbanization presents a major threat to biodiversity [1,2]. By 2050, 68 percent of the world's population will live in urban areas [3]. As urban settlements increase, the landscape undergoes drastic change from its pristine state [4]. However, ecologically speaking, urban areas are highly modified and fragmented habitats, in the form of several managed and unmanaged urban green spaces, like public and private garden, nature reserves within the city, vacant plots, to name a few, which are capable of providing resources to a small number of highly adaptable species of fauna [2,4–6]. Not only resident, but several migratory, species make use of this urban habitat [7]. The urban avian community is composed of introduced and invasive species and highly adaptable native species [8,9], although Aronson et al. [8] observed that the community is dominated by locally adapted species, with only five percent non-native species. The urban greenspace along with the biodiversity it harbors, forms a unique ecosystem within the human dominated landscapes, capable of providing several ecosystem services to the cities [2]. Ecosystem services are the services that are beneficial to humans as a result of naturally occurring processes [10], which render them all the more important in human dominated landscapes, like cities.

Birds, which are some of the most successful urban adapters, provide a range of ecosystem services. Birds, in general, are capable of significantly affecting ecosystem processes, due to their specific characters, like flight capability, high metabolic demand,

which leads to tolerance to discontinuous food sources; and, flock formation, which significantly affects ecosystems processes, like nutrient cycling [10]. The urban bird community structure also acts as an indicator of the structure and functionality of urban areas as habitats [11]. In this study, it was found that habitat specialists, like woodpeckers and hole-nesting birds, occurred in the peripheral areas of the city, indicating healthier vegetation cover, while habitat generalists increased near the city center and residential areas with less vegetation cover.

Birds have been found to provide all four types of ecosystem services that were mentioned in the UN millennium ecosystem assessment, namely, regulatory, provisioning, supporting, and cultural [10]. Urban birds provide regulatory services by acting as pest control agents when they feed on disease causing insects, prey on rodent population, and scavenge on garbage; provisioning services by acting as seed dispersers when they ingest fruits, which helps in plant regeneration; and, supporting services by acting as nutrient recyclers via their excretory products [12,13]. However, urban birds perhaps play the most crucial role in providing various cultural services. One of the most important services rendered by urban birds is to act as a connecting link between the natural environment and the increasingly nature deprived urban denizens [7]. Birds in residential neighborhoods in cities are generally valued for their color and songs, for providing mental and physical wellbeing, as indicators of seasonal change, for education, and for giving sense of familiarity, by the residents [7,14]. Birds are also an inspiration for art, recreational activities, like birdwatching and wildlife gardening [10]. In India, it is a tradition of grain merchants to give a small portion of their goods to granivorous birds, like house sparrows (*Passer domesticus*), as an offering for prosperity in business. In the city of Delhi in India, it is a common practice of offering meat to scavengers, like black kites (*Milvus migrans*) as religious practice, due to which the black kite population dynamics in the city is significantly affected [15].

It is abundantly clear that the conservation of these ecologically important fauna in urban landscapes is crucial. Many cities are now experimenting with the management of urban green spaces for conservation and, there have been numerous studies on the effect of such management interventions on bird ecosystem services in cities [13]. However, for such management practices to be entirely successful, it is also important to understand the uniqueness of birds who call this urban habitat their home. One is then compelled to ask what characteristics sets apart the birds able to adapt to this unique habitat from those who disappear from it? It would be counter-intuitive to the purpose of conservation if such measures are taken without understanding the changes in “traits” of urban birds.

Studies on trait changes have grown in recent years, as researchers begin to focus on the study of urban areas as modified habitats. It has been suggested that studying the traits of urban biodiversity could be a more effective approach for preserving the ecosystem functions and services in urban areas, as such data provide authentic and useful information to urban planners [12]. Birds comprise the taxon that is perhaps the best studied in cities. Birds constitute especially useful model species for studying trait changes, as they respond to changes rapidly, are of interest to naturalists and the public at large, are easy to monitor, and they show measurable changes. They have hence been studied widely in the urban context [16,17].

McKinney et al. [1] conducted the last comprehensive review assessing diverse trait changes that were observed in urban birds. . In general, only certain species, which are characterized by specific traits or combinations of traits, seem to be more capable of coping with the environmental alterations that are imposed by urbanization [18]. This capability might differ according to season, geographic region, or city structure [9], but such species of urban utilizers can tolerate a wider range of environmental conditions [19] and they appear to exhibit similar characteristics globally [20,21]. The research on bird adaptations to urban habitat has since expanded considerably. Many researchers have carried out reviews and meta-analyses of specific trait changes, including behavioral traits [22,23],

community traits [21], and physiological changes [24]. However, there is a need for an updated comprehensive review that collates and synthesizes existing information.

This paper reviews research studies on traits that influence the survival and response of birds to urbanization, based on a literature review of research that was conducted between 1979 and 2020, identifying the state of current knowledge, highlighting key knowledge gaps, and identifying geographic and species-specific disparities in research that require specific focus. The specific aim of this study was to synthesize the information available on studies when comparing urban and rural birds while taking a trait-based approach. Finally, we highlight the gaps in knowledge and pinpoint future directions for research.

2. Materials and Methods

We listed and categorized the traits that are described in birds referring to the review paper by McKinney [1] and making additions of our own. The traits were selected with the knowledge that they were essential for basic survival and reproductive success of birds. To begin this review, we conducted an intensive literature search for each trait, using Google Scholar during August 2019, based on combinations of the following keywords: “urban”, “birds”, “urbanization”, “impacts”, “traits”, “changes”, “effects”, “behavioral”, “physiological”, “functional”, “diversity”, “global”, “avifauna”, “song”, “life history”, “nesting”, “foraging”, “generalist”, and “specialist”. Each publication that resulted from this search was reviewed to determine whether it met the criteria for inclusion. The basic criterion was that the study had to be either a comparative field study or an experimental study looking at effects of urbanization in an urban-rural gradient on bird communities or a single bird species. The literature was searched by its importance and relevance to the key words used. Review papers and experimental studies were included as a part of this study. The reviewed papers were grouped into five broad trait groups: ecological traits, which included traits pertaining to ecological niche and community interactions; life history traits, which included traits that are related to reproductive success, breeding cycles, and overall survival; physiological traits, which were related to the physiological, endocrine, and morphological changes in the birds in urban areas; behavioral traits, which were the changes in important behaviors, like singing, fear responses, innovative behavior, to name a few; and finally, genetic traits, which were the trait changes in the genetic structure of urban birds (for complete list, refer Supplementary Materials: Table S1). Each paper was read and categorized based on the methodology used, the results, and interpretations of the study. Knowledge gaps and scope for further research were documented.

3. Results

A total of 226 publications were finally included for review (Supplementary Materials: Table S2). The earliest paper that we found was published in 1979. The field has grown rapidly since then, with research on several different traits (Figure 1; Table 1). The interdisciplinary nature of the topic has led to an expansion in the number of journals publishing urban ecological research (Supplementary Materials: Figure S1). Behavioral Ecology published the most papers on trait adaptations in urban birds, followed by Urban Ecosystems, PLoS ONE, and Scientific Reports (Supplementary Materials: Figure S1). Many of the trait changes have been studied on large bird communities at the regional or global scale. Song birds and water birds are well studied, and most of our understanding of impact of urbanization comes from these guilds of birds (Table 2). Additionally, some bird species such as Eurasian blackbird (*Turdus merula*) are widely represented in the literature as compared to others. Studies from temperate countries dominate the literature, with only a few studies from the tropics (Figure 2).

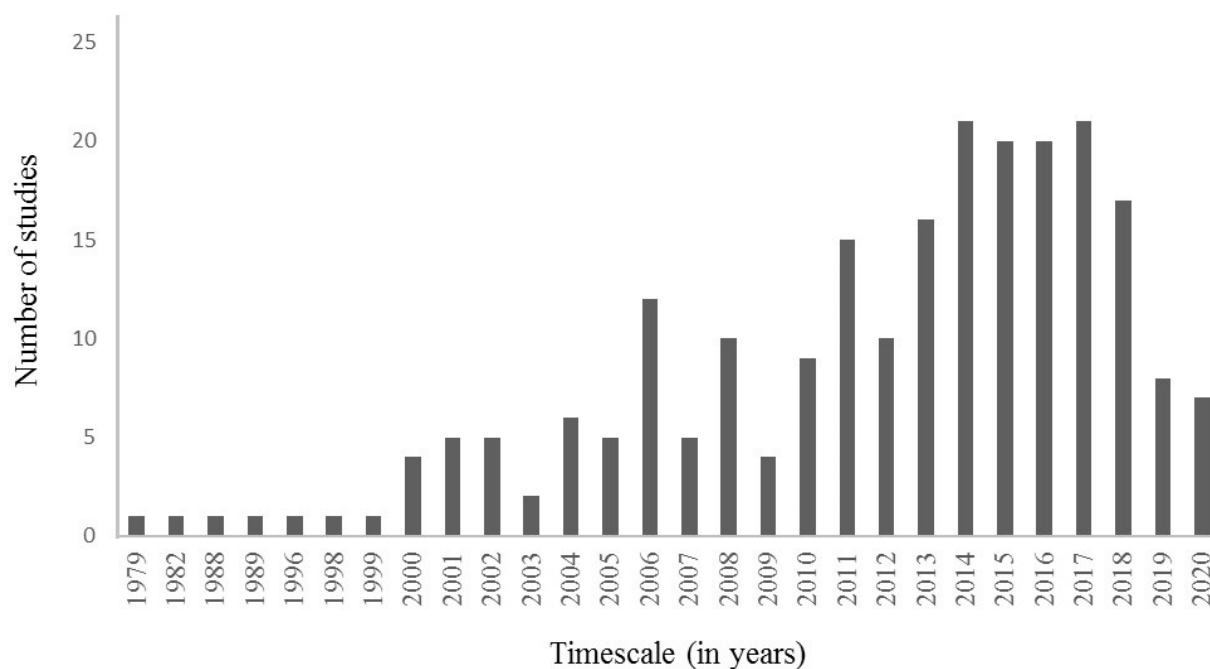


Figure 1. Number of research papers on urban bird traits related to urbanization from 1979 to 2020.

Table 1. Number of published articles on each of the bird traits included for this review along with the number of studies on individual species (<4 species) or large communities (>4 species).

Trait Studied	Number of Studies (<4 Species Studied)	Number of Studies (>4 Species Studied)	Total
Ecological			
Diversity	1	14	15
Nesting spaces	7	9	16
Abundance		8	8
Richness		10	10
Diet breadth	1	9	10
Generalist-specialist	5	7	12
Distribution pattern	1	3	4
Density		3	3
Migration	4	3	7
Habitat dependence	1	4	5
Dispersal		1	1
Sociality and sedentariness		1	1
Community composition		1	1
Habitat preference	2		2
Life history			
Reproduction cycle	3	2	5
Clutch size	5	4	9
Nesting success	4	2	6
Breeding timing and/or performance	2	1	3
Brood size	2	2	4
Fecundity and adult survival	2	1	3
Activity time range	1		1
Migration		1	1
Fitness	1		1
Physiological			
Reproductive physiology, circadian rhythm and migration	12	12	24
Brain size	1	5	6

Body size and/or mass	5	4	9
Inflammatory response, oxidative stress	1	2	3
Stress physiology	10	1	11
Endocrine traits		1	1
Bill length	2		2
Plumage coloration	1	1	2
Behavioral			
Fear and stress responses	17	10	27
Foraging behavior innovation	6	6	12
Innovation, learning and problem-solving ability, Neophobia and risk assessment	10	5	15
Entire song structure	7	3	10
Song frequency and/or amplitude	16	1	17
Aggression	11		11
Dawn chorus	1		1
Call frequency, amplitude	2		2
Song frequency, bandwidth	2		2
Song syllable	1		1
Song timing	1		1
Genetic			
Gene expression	2		2
Genetic changes	1	1	2
Genetic divergence	1	1	2
Total	148	139	

Table 2. Bird families represented in the literature studying urbanization induced trait changes. Bird community studies comprise of global reviews or analysis of global datasets, while individual family studies comprise of local datasets and experimental studies.

Bird Family	Common Name	Ecological	Life History	Physiological	Behavioral	Genetic	Total
Bird community (>2 families)		58	7	15	29	2	111
Turdidae	Thrushes	1	1	8	8	2	20
Passerellidae	New world sparrows		1	7	11		19
Paridae	Tits		3		11	2	16
Passeridae	Old world sparrows			3	5		8
Fringillidae	Finches				6		6
Cardinalidae	Cardinals				4		4
Corvidae	Crows	1	1	1	2		5
Strigidae	True owls	3	1		2		6
Zosteropidae	White-eyes				4		4
Accipitridae	Accipiters	2	4	1	4		11
Mimidae	Mimids			2	1		3
Rallidae	Rails				3		3
Emberizidae	American sparrows			2			2
Muscicapidae	Old world flycatchers				2		2
Sturnidae	Starlings				2		2
Troglodytidae	Wrens			1	1		2
Tyrannidae	Tyrants flycatchers		1		1		2
Tytonidae	Barn owls	2	1				3
Artamidae	Crows				1		1
Columbidae	Pigeons and doves				1		1
Corcoracidae	Australian mudnesters	1					1
Falconidae	Falcons and caracaras	2	3		1		6
Icteridae	Songbirds				1		1
Laridae	Gulls			1	5		6
Meliphagidae	Honeyeaters				1		1
Monarchidae	Monarch flycatchers				1		1

Nectariniidae	Sunbirds			1			1
Thraupidae	Tanagers				1		1
Pandionidae	Ospreys				1		1
Haematopodidae	Oystercatchers	1					1
Total		71	23	42	109	6	251

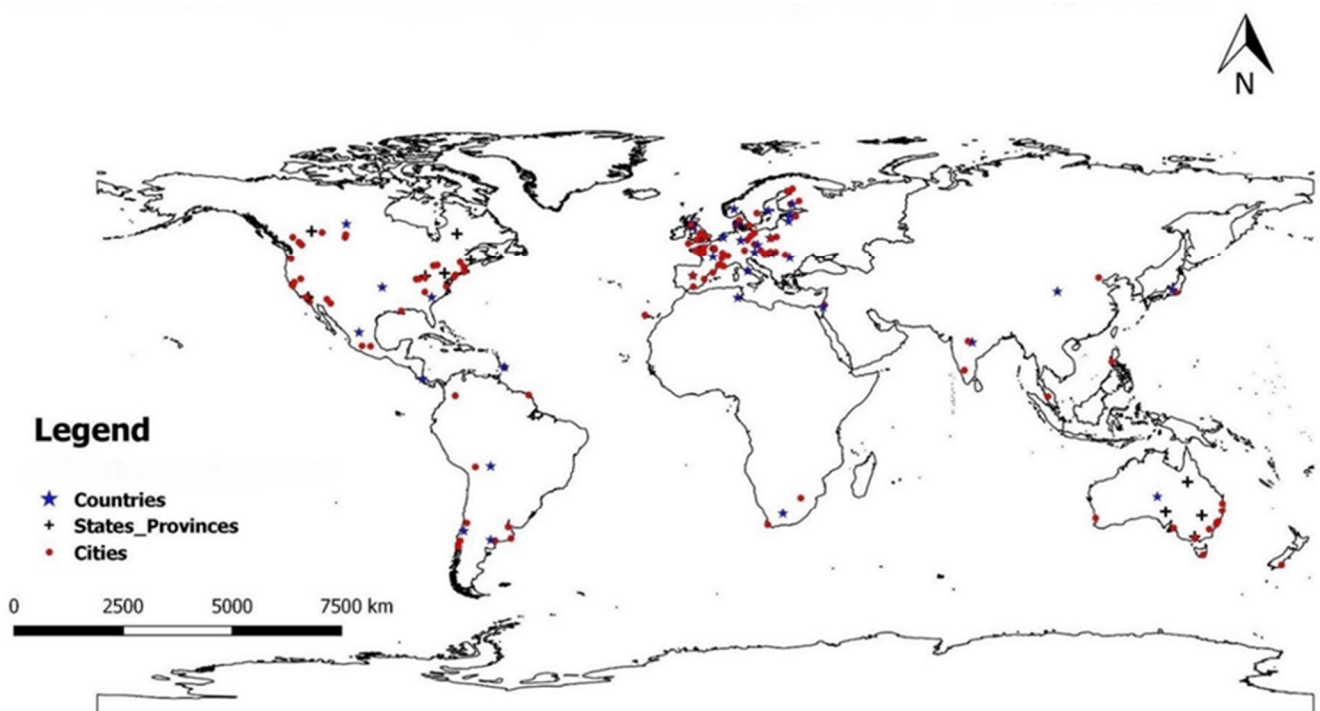


Figure 2. Distribution of research studies on urban bird traits across the world. Studies carried out at state or province level included multiple cities which were not specified in the publication.

3.1. Ecological Traits

3.1.1. Bird Diversity and Abundance

An overall decrease in diversity from rural to urban areas [25–27] as well as an increase in abundance of only a small subset of species are some of the most important ecological effects of urbanization on birds. One study observed a decreased overall abundance of birds in urban areas [28]. Species richness also shows a decreasing trend with an increase in urbanization, a pattern observed globally [29,30]. A study encompassing several cities in Europe observed that urban bird communities also showed lower evolutionary distinctiveness than rural communities [31]. A global review observed that, despite the loss of forest dependent or native species in urban areas, the functional diversity remained the same [32].

The species richness and density of seasonally migrating species also reduces with an increase in built infrastructure [33,34]. Many birds, such as Eurasian blackbird and house sparrow, show a loss in migratory behavior, as there are enough food resources available in urban areas to support them through the winter months. Such a trend may eventually lead to reduced richness in urban areas [35]. Birds with specific dietary requirements may also avoid migrating to cities because of a lack of adequate food resources. For example, insectivorous birds might find difficulty in finding insects in cities, thus reducing their urban population [35,36]. Studies also speculate the indirect effects of urbanization on resident vs. migrant bird dynamics. Resident species may occupy good quality nesting sites in cities before migrants arrive, thus driving migrants away from urban areas by competitive exclusion [37].

3.1.2. Generalism—Specialism

Specialist species are more likely to be negatively affected by change than generalists [38–40]. Devictor et al. [41] found that generalists, which use multiple habitats in the landscape matrix, are less affected by habitat fragmentation than specialists, which are dependent on one or a few habitat types. Generalists should benefit from disturbed landscapes, as there will be reduction in competition from specialists, who do well in stable environments and, hence, will be negatively affected by a degradation in landscape [42,43]. Generalist species usually have large niche breadths, lay multiple clutches, and have broad diets, which makes them more successful in cities [39]. This indicates that, to understand whether a bird can cope with urbanization, we need to consider the effects of multiple traits together.

Whether a species is a generalist or a specialist is largely due to the ability of these birds to adapt to feeding and nesting preferences, as described further below.

3.1.3. Diet Breadth

Diet breadth is one of the most important traits affected by urbanization [44,45]. Bird species that feed on fruits and grains tend to increase in numbers in urbanized areas as compared to insectivorous species [37,46,47]. This might be because cities have a substantial proportion of fruiting trees [48]. Similarly, a review on urban raptors suggested that urban areas are typically inhabited by raptors that are feeding on forest dwelling birds, due to a prevalence of large trees in cities, but open-area raptors feeding on grassland species do not generally inhabit urban areas [49]. Raptors feeding on rodents and scavenging raptors also show similar foraging, depending on the availability of suitable prey or carrion [50–52].

In many countries, there is a culture of putting out bird feeders, supplementing bird diets with seeds, nuts, and grains [53]. Granivorous birds benefit from this and, hence, do well in urbanized areas [27,37]. Callaghan et al. [39] observe that insectivorous and granivorous birds avoid urban areas, a phenomenon that requires further investigation in order to assess whether it is specific to countries where feeding birds is not a popular activity.

Kark et al. [44] report that, in downtown areas, most of the birds were omnivores, especially in temperate countries. Similarly, urban bird composition in Santiago, Chile, predominantly consisted of omnivorous and granivorous species [47]. Omnivorous species, like Eurasian blackbird, great tit (*Parus major*), and house sparrow, are commonly studied in urban avian ecology research (Figure 3). Again, omnivore birds are likely to feed on food scraps, discarded food items and, thus, seem to be possibly making use of the food resources that are discarded by humans. Apart from food preferences, urbanization can negatively affect birds exhibiting solitary feeding behavior [39]. Many birds show subtle changes in foraging behavior in order to adjust to the novel foraging sites. Ground foraging and insectivorous birds forage differentially in suburban remnant patches vs. continuous vegetation [54].

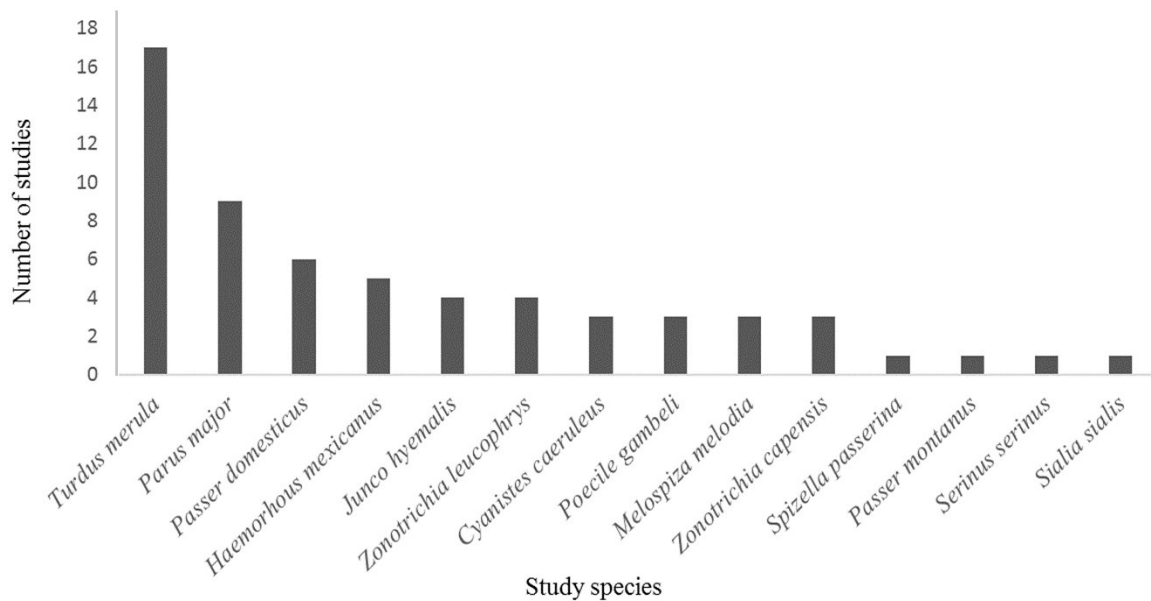


Figure 3. Most commonly studied bird species for urbanization induced trait changes.

3.1.4. Nesting Sites

The utilization of nesting sites is an important factor determining the success of bird species [45]. One of the most consistent effects of urbanization is on ground-nesting birds, whose abundance consistently decreased across most of the studies [16,55]. Small sized ground nesters are most impacted by urbanization in Australia [56]. Birds that nest on high trees and in tree cavities have a better chance of survival in cities [37,57]. Studies speculate that urbanization does not necessarily increase the availability of cavity nesting sites. However, cavity nesters might be less prone to predation, because of their nesting habit, hence surviving better in cities [37]. Alternatively, cavity nesting birds might be using artificial nesting sites, such as nest boxes provided in cities. Cities with good tree cover will benefit birds that nest on trees, as there will not be a scarcity of nesting sites.

Birds that are more adaptable and use a variety of nesting strategies like making use of man-made structures, are more likely to do better in urban areas as compared to birds with specialized nesting preferences [58–60]. Adaptive nesting strategy also ensures better productivity, as is seen in the urban peregrine Falcon (*Falco peregrinus*), as many artificial structures provide better protection against predators or the elements [61]. Consequently, species that are adapted to urban conditions show higher abundance in urbanized areas [8,59,62]. Other birds, such as open-cup nesters, which require trees and shrubs to support their nests, are negatively associated with urbanized areas [59].

3.2. Life History Traits

Life history traits, such as clutch size and brood success, have a considerable positive impact on bird populations in urban areas [37]. Many urban species show an increase in the clutch size and brood size [63]. The increase in number of eggs and chicks helps these birds to overcome the losses that occurred during predation or the effects of urbanization such as mortality caused due to collision with cars or windows [37,61]. Urban birds tend to lay eggs earlier than their rural counterparts [64–68]. This might be because of the improved resource availability in cities. There are exceptions; Chamberlain et al. [69] found that, even though results vary from species to species, most urban bird populations are characterized by slightly greater annual productivity and lower nestling weight. However, certain species do not show such a pattern. For example, Marini et al. [70] find that clutch size does not differ in mountain chickadees (*Poecile gambeli*) as one moves along the

urban-rural gradient in North America. Similarly, in magpies (*Pica pica*), a European species, the clutch size does not vary as one moves across the rural to urban gradient [71]. Brood size and nestlings per nesting attempt did not show a consistent pattern of differences between urban and non-urban areas [69]. Some raptor species also fledged fewer offspring in urban areas when there was a lack of prey or excessive human disturbance [68].

3.3. Physiological Traits

3.3.1. Body Mass, Size, and Plumage Coloration

Birds may produce large broods in urban areas, but the condition (average body size, morphological features) of offspring is poor, because there is a high chance of survival, even for the low-quality offspring [72,73]. The change in diet preferences might be associated with higher survival rates, but poor body condition. Birds have ample resources available throughout the year in the city, which is perhaps the reason they do not accumulate more body fat. Another possible reason is that temperatures in cities are higher due to urban heat island effects; hence, birds have smaller sizes: as theory predicts that as temperatures drop, body size increases [73]. Adverse ecological effects may also constrain the body size or condition of offspring [73]. Nestlings in urban habitats are fed less amount of food, or lower quality food, and they reach a lower body mass [74,75]. However, the urban area-smaller mass relation is not observed in all urban birds. A study on silver gulls (*Larus novaehollandiae*) in Tasmania found that adult male gulls in urban areas had greater body mass than adult male gulls in rural areas [76]. Perhaps omnivorous species show an opposite trend in terms of body mass due to the consumption of a wide variety of foods.

Liker et al. [75] found that house sparrows were larger in rural areas as compared to urbanized areas. Sparrows in the Budapest city center were more than 5% lighter than sparrows at the least urbanized locations, and the leanness of urban birds was detectable, even when they compared differently urbanized habitats with similar utilization [75,77].

Although the literature on body size and mass of urban birds is comprehensive, research is only now emerging on changes in plumage coloration in urban birds. A recent study across three cities in Argentina showed that the amount of built area negatively affected the color diversity of bird communities. Hence, the bird community in the city was predominantly composed of grey colored species [78]. Urbanization selects for birds with similar colors, primarily those matching the surrounding habitat. Because plumage coloration is an important trait, not only for the reproductive success of birds, but also as a camouflage to avoid detection, it is important to be studied on a larger spatial scale.

3.3.2. Brain Size

Birds and mammals with relatively larger brain size may be associated with the ability to invade novel habitats [79,80]. Callaghan et al. [39] hypothesize that birds with large brain size might be favored in cities and, hence, such birds should be successful in urban environments. Theory predicts that larger brains might be advantageous to individuals in dealing with altered environments and it might help in innovative behavior and learning [81]. Larger brain size implies that individuals might be more able to explore novel environments and food resources, helping such birds adapt to city life [5]. However, experimental studies suggest that there is a lot of variation in brain size and success in urban environments [82,83]. More work is required in order to definitively declare whether brain size is actually related to success in urban environments.

3.3.3. Stress Response Physiology

Urban birds are exposed to a variety of stressors, like traffic noise [84,85], artificial light pollution [86,87], uneven food distribution, and chemical pollution [85,88]. Stress response to such disturbances is indicated by the level of plasma corticosterone hormone (CORT) secretion [24,84,89–91]. Many studies have revealed changes in the baseline and

induced corticosterone levels in birds in response to urban stresses [85,88–90]. The Eurasian blackbird female shows an increased corticosterone secretion in response to artificial light exposure [86], even though Partecke et al. [88] had observed an overall decrease in corticosterone secretion in urban blackbirds. Urban birds also show reduced corticosterone secretion in noisy environments when compared to rural populations, as is displayed by song sparrows (*Melospiza melodia*) [84] and house wrens (*Troglodytes aedon*) [85]. Reduced corticosterone in urban birds is associated with low protein diets [85]. The decrease in CORT secretion in species that have colonized urban areas for a long time could be due to habituation to these stressors [84,86,89]. When male song sparrows from different parts of city were compared for CORT levels, they did not show any difference, which further indicates that these urban song sparrows might be adapted to urban stressors [84]. Bonier [24] reviewed the various endocrine trait changes in urban birds and found no consistent pattern in stress hormone change in all urban species. Even within the populations, the differences fluctuated according to the age and life history stage.

Elevated levels of baseline corticosterone may have a considerable effect on other behavioral and physiological functions. Brain Arginine Vasotocin immunoreactivity, which is associated with various functions, like territoriality and social behavior, differs in response to changed plasma corticosterone in urban curve-billed thrashers (*Toxostoma curvirostre*) [92].

3.3.4. Reproductive Physiology

Living in urban areas influences reproduction in birds [24,93–96]. A global analysis of passerine species found that sexually dichromatic species were less likely to occur in urban areas [97].

Urban populations of Abert's towhees (*Melospiza aberti*) are found to have greater plasma luteinizing hormone (hereafter plasma LH) than rural populations [67]. This leads to urban birds developing gonads earlier, starting breeding earlier, and having a prolonged breeding season than rural birds [64,66,67,98–100]. Having a prolonged breeding season might help in the production of more broods and, thus, might be an important trait to have in urban areas to successfully colonize them. Such earlier gonadal development is also prominent in resident rather than migratory birds, as observed in the males of urban Eurasian blackbirds [101] and dark-eyed juncos (*Junco hyemalis*) [101].

Partecke et al. [64] suggest phenotypic plasticity in response to several new conditions, like artificial lights, in urban areas to be the primary reason for this change. Birds living in temperate regions are especially dependent on day length and duration of natural light for their reproductive development [95,98,99]. The presence of artificial light in the city habitat plays a major role in the earlier growth of gonads in male birds [66,87,98,99,102,103]. However, low levels of artificial light inhibit the secretion of plasma LH in male western scrub jays (*Aphelocoma californica*) [91,95]. Apart from artificial light, differential food availability could also affect the pattern of plasma LH physiology [69,91].

Factors, like the vegetation structure, replacement of native plants by exotic species, habitat fragmentation, predatory pressure, and food availability, influence the life history traits of urban birds [69,104]. The reason for lower clutch size in urban compared non-urban areas could be because of lower availability of high quality or specialized food in urban areas, especially during chick development [105]. Such deficiency in good quality food could also lead to increased competition between conspecifics during breeding season, affecting clutch size [69].

Such changes in reproductive physiology could affect life history traits, like fitness levels and nesting success of urban birds [98,99]. A prolonged breeding season could also be favored by urban birds, leading to fewer birds migrating for breeding [64,101].

3.3.5. Immune and Inflammatory Responses, Oxidative Stress Response

Physiological responses to various stressors in cities contribute to oxidative stress in urban birds [106,107]. Increased oxidative stress exposes birds to different types of diseases and organ degeneration [107]. A comparative study of blood and liver transcriptomes for these stress responses revealed that most of the genes for this stress response were expressed in a higher amount in urban birds [108]. An increase in blood antioxidant levels helps urban birds to tolerate such stress [106]. Successful urban colonizers use also genetic and epigenetic mechanisms, DNA methylation, and histone changes to cope with oxidative stress [107]. Urban Eurasian blackbirds developed lower oxidative stress when compared to rural populations, indicating an adaptation to high stress levels [109].

Physiological traits also closely influence behavioral traits: hormone secretion is associated with reproductive behavior, and brain size with innovation.

3.4. Behavioral Traits

3.4.1. Song Structure

One of the major characteristics of urban areas is the increase in low frequency noise levels, such as from traffic [110,111]. Birds in urban areas are impacted by noise in the low frequency range, as it carries over longer distances [111,112]. Low frequency anthropogenic noise tends to mask bird songs, which leads to poor song transmission, and, ultimately, poor reproductive success. Perhaps one of the most widely documented phenomena in behavioral trait changes in birds in response to urbanization is the modification of song and call structure to avoid such masking (Figure 4).

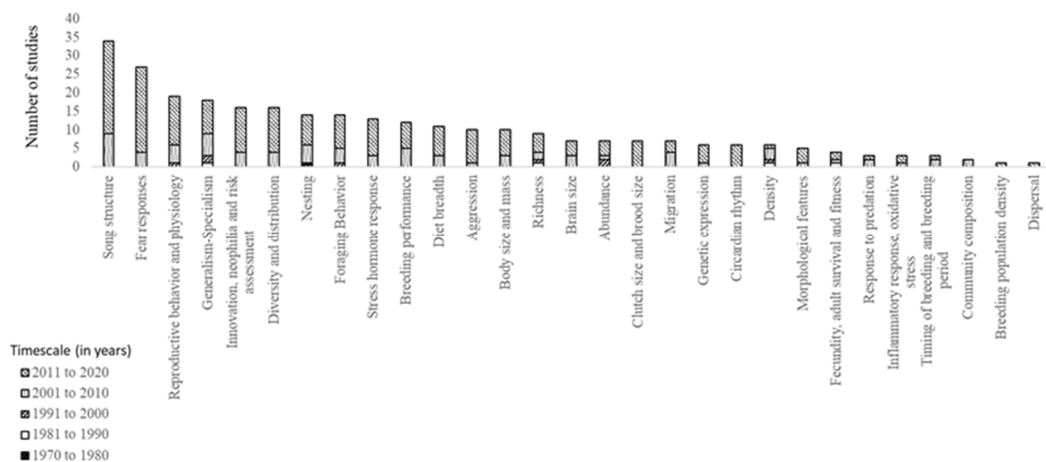


Figure 4. Proportion of studies in each decade from 1970 to 2020 on different trait changes due to urbanization.

There are thought to be two mechanisms by which birds alter their song structure. One school of thought suggests that birds sing at higher frequencies in areas with high anthropogenic noise levels, as shown by studies on several species of song birds across different continents (e.g., [113–117]). In fact, high frequency songs are one of the selective forces for species to occupy urban habitats [118]. However, this mechanism might not always be effective for reproductive success [119–122]. White-crowned sparrow (*Zonotrichia leucophrys*) change song frequency and bandwidth, which leads to a reduction of vocal performance, which is deleterious for mate attraction and territory defense [120,122].

Some birds also increase the amplitude of their songs, a phenomenon called “Lombard effect”, in order to be heard above the city noises [111,123–126]. Great tits and Eurasian blackbirds are classic examples exhibiting this phenomenon [111]. Changes in bandwidth, trill rate, number of song syllables, and time spent singing have been documented in some birds, for effective song transmission [121,122,127–129]. Urban European robins (*Erithacus rubecula*) sing nocturnally in order to avoid song masking [35,110]. The alarm call structure is also modified due to masking. Urban silvereyes (*Zosterops lateralis*) had

lower average, maximum, and minimum frequencies than rural birds [130]. Silvereyes also showed decreased syllable rate in Australia [131].

Apart from traffic noise, reflective structures, vegetation density, ambient temperature, and temporal changes in noise levels due to human activities also affect song communication in birds [132,133]. Male house finches (*Haemorhous mexicanus*) in an urban park in California sing at higher frequencies in areas with higher pedestrian traffic [134]. In the case of the great tit, this phenomenon is attributed to either large scale evolutionary or ontogenetic shift or a local scale song learning from neighboring males [112,113]. Morphological changes, like change in bill structure, due to differential food type in cities, could also change song structure [135].

Urban noise and artificial light levels affect the dawn chorus of urban bird populations [136,137]. Males of four out of five songbird species residing near street lights started singing earlier in the day. This increased their extra pair copulation success, but led to females selecting unsuitable mates [138]. Other studies found that more than artificial light, anthropogenic noise is responsible for temporal shift in the dawn chorus of the study species [117,136,137].

3.4.2. Boldness and Tolerance to Human Presence

Urban habitats have a constant presence of humans and vehicles, altered refuge patches, and differential predator composition [139–144]. Flight initiation distance (FID) is a standard measure for estimating the boldness and tolerance of birds to potential threats in urban areas [23]. Urban birds are observed to be bolder and more tolerant of human and vehicular approach, as they exhibit shorter FIDs [145–152].

A shorter FID reduces the cost associated with flight, and it can help birds exploit novel food sources. Several species of gulls have shown shorter FID in the proximity of human food sources [153–155]. In a study on 39 urbanized species of birds in Europe, urban birds had shorter FIDs than rural counterparts. [156]. This study also showed that the urban bird community had a larger variance in FID when compared to rural bird communities, but this variance decreased with increase in time since urbanization. This means that most of the birds adapted to the threats in urban areas as the time since colonization increased.

Along with FID, urban birds have also adapted to the predation threat of feral animals, like cats and dogs. Urban Eurasian coots (*Fulica atra*) portrayed the same amount of vigilance in the presence of domestic dogs as their natural predators [139].

Behavioral plasticity, which is the inherent ability of an organism to change in response to external stimuli, is one of the main characteristics exhibited by birds who are capable of changing their fear responses. This is thought to be an important adaptation to possess in urban areas. [157–159]. However, it has been argued that habituation induced change is not the reason for the higher tolerance of humans in urban areas. Those individuals who already had a bold personality in their natural habitat were able to colonize urban areas, while others were unsuccessful [82].

3.4.3. Neophobic and Innovative Behavior

Urban areas provide novel types of food resources in the form of artificial feeding or garbage dumps [153,160–162]. Novel urban food sources also come with new types of risks in the form of feral cats and dogs [160,163–165]. Not all native birds have the ability to exploit such sources of food—it seems that bird species with innovative capability and bold personality have an increased capacity to thrive [152,166–168]. Several species of gulls exhibit a great ability to exploit human provided food, for example, by adjusting their foraging time according to peak human activity timing, like school breaks or waste center opening time [169]. Not just foraging innovation, but certain urban species, like Indian house crows (*Corvus splendens*), also show innovative nesting behavior after nesting failure during breeding season [170].

Successful urban colonization requires a balance between neophilia and neophobia [162]. Urban great tits are more tolerant towards a novel object that is placed near their feeders than rural individuals [165]. However, two different studies on house sparrows in Hungary and mountain chickadees in Reno, USA indicated no reduction in object neophobia in urban populations [171,172]. Griffin et al. [162], in a review, suggested that neophilia/neophobia and boldness might be species specific. Corvid species were more neophobic towards novel objects than non-corvid species [173].

Exposure to pollutants and inferior quality food during chick development might also affect the ability to exploit novel food sources as well as learning from parents and conspecifics [162,167]. Research pin pointing the factors influencing the ability to exploit novel urban resources is required.

The ability to innovate different foraging techniques is crucial for successful urban colonization by birds [160,168,174]. The rate of innovation seems to be stronger during early invasion of novel urban areas [5]. The rate of innovativeness also seems to predict the risk-taking ability of the species [168]. The rate of innovation has also been linked to brain size in some urban birds, which also assists in successful urban colonization [175]. Innovative foraging also leads to changes in dominance hierarchy, behavioral strategies that are based on human movement, and introduces new types of competitions [176].

3.4.4. Aggression

Aggressive behavior can be displayed towards competitors [176–179], can be food related [180], due to exposure to chemical pollutants [181], or during nest defense [182]. Urban great tits were more aggressive towards competitors, but they exhibited inconsistent reaction towards a simulated competition when compared to their rural counterparts [179].

Urban great tits also showed greater distress behavior when threatened [183]. In another study on northern mockingbird (*Mimus polyglottos*), urban birds that were exposed to higher amounts of lead were more aggressive towards simulated competition [181]. In Eurasian coot populations residing in the same urban area, older and more established populations were consistently more territorially aggressive than recently colonized population [184]. Urban sparrowhawks (*Accipiter nisus*) showed more aggressive nest defense than rural sparrowhawks [182]. These changes might not be just behavioral adaptations, but a consequence of micro-evolution over the years in these birds causing changes in the behavior. However, differences in territorial aggression in urban birds appears to be species and situation specific. The species that show increased aggressive behavior in urban areas also generally exhibit bolder personality [155,176].

3.5. Genetic Traits

Although phenotypic trait changes in birds in response to urbanization have been extensively studied, solid evidence for genetic basis for such phenotypes is limited. Studies have focused on finding out the genetic modifications behind observed physiological trait changes like inflammatory and oxidative stress response, morphological trait changes, like change in wing structure, behavioral changes, like risk assessment, migration and urban invasion by certain functional groups [107]. The urban populations of great tits in Europe had elevated gene expression for inflammatory, oxidative stress, and detoxification responses [185]. Similar results were obtained for urban blue tits (*Parus caeruleus*) [186].

Urban Eurasian blackbirds have undergone genetic divergence at a locus coding for risk avoidance [187]. Human induced changes in habitat, along with various stressors, like the presence of novel predators, traffic noise, and pollutants, have led to accelerated changes in genotype in urban populations when compared to rural populations, with the potential to create genetic divergence between urban and non-urban populations [185]. However, an attempt to study the differences in overall genetic composition of Eurasian blackbirds yielded negative results [188]. This suggests that genetic differences between

urban and rural populations have only occurred in selected genes, based on adaptive requirements. Urban blackbirds diverged from their rural populations at a single loci coding for risk avoidance [187]. However, there is still little evidence for urbanization-induced micro-evolution.

4. Discussion

Some bird traits are beneficial for their survival in cities, while others could be harmful. This review demonstrates that the impact of urbanization on birds is immense: and yet, our understanding of it is still poor. It is evident that studying one trait might not give a complete picture of how urbanization might affect birds or populations, but looking at a combination of traits would provide more insights.

Behavioral trait changes are dependent on plasticity, individual personalities of the bird populations, and, at least for a few species, the development of separate cognitive skills that are specific to urban needs [22,170]. In particular, as our review demonstrates, behavioral trait changes in urban birds are often a combination of two or more trait changes. Such correlated changes create behavioral syndromes in urban birds [171]. An example of such behavioral syndromes is the occurrence of increased aggression in birds with bolder personalities [176].

The consequences of trait change have not yet been studied in detail, and they require attention. Urban birds could incur energetic and reproductive costs due to changed corticosterone levels or increased aggression in urban areas. The ability to establish a successful breeding population in novel environments also depends on the population size and selection pressure [22]. Earlier and prolonged breeding seasons could have negative effects on reproductive health of urban birds, especially females. Therefore, even though, in the short term, birds might be adapting to urbanization by producing more broods and laying more eggs, we need to understand whether these birds will be successful at surviving in cities in the long term. Additionally, it is important to understand the reasons behind some birds showing a reduction in clutch and brood size in urban areas. Long term data collection is needed for monitoring the population of birds inhabiting the cities. Popular citizen science initiatives can help to answer some of these questions.

In the context of physiological and morphological trait changes, the literature suggests changes in stress hormone levels and reproductive hormone levels. The reason for the lack of consistent pattern in the differences in hormone levels in urban and non-urban populations could be due to the selection of physiologically plastic species in urban areas, which affects the life-history traits and ultimate density of the populations. This could mean potential extinction of species that are currently residing in urban areas, but are not able to adjust their physiology to the novel environment [24]. However, the effect of such differences in hormone levels on the overall fitness of the bird species that are successful in changing their endocrine traits has not yet been investigated in detail.

Trait changes in response to urbanization have the potential for creating genetic divergence between urban and rural populations of a species. The most important trait change contributing to genetic divergence is the change in reproductive behavior. A combination of different traits, like singing behavior, timing of reproduction, and nesting success, play a role in the reproductive pattern of birds. Urban areas modify these traits. Song birds possess high phenotypic plasticity and they have changed song structure in response to urban noise. Trait changes, coupled with isolation due to habitat fragmentation further leads to disconnect between urban and rural populations, leading to differential trait development in both populations. There is already evidence to suggest changes in genetic makeup at certain loci in urban and rural populations. Geographical isolation, coupled with high phenotypic plasticity, has a potential for further genetic divergence in urban birds. Large scale spatial and temporal studies, investigating such microevolution due to urbanization, could help in predicting the course of genetic divergence of urban bird populations in the future. Studying such urbanization induced genetic trait changes could help not only in conserving biodiversity in cities, but could also help to answer some

of the basic questions in evolutionary ecology and also help in conserving the ecosystem services in cities [185].

There is a large gap in our knowledge regarding the effects of urbanization on birds in tropics, despite the fact that tropics support many more bird species and they are growing rapidly in terms of urbanization [55]. Future research in this area could also differentiate between introduced species and native species, in order to understand whether the traits discussed in this review contribute to the success of introduced species.

A lack of information regarding how urbanization will affect avifauna in urban tropics can be a major impeding factor while designing conservation strategies to protect the biodiversity in these ever-growing cities. Moreover, a study on southeast Asian cities found that, the wealthier the cities get, the richer they become in terms of urban green-spaces and natural aesthetics [189]. This could lead to potential habitat generation in growing cities, further affecting the bird traits.

Studies have started to emerge on the effect of urbanization on the traits of diurnal and nocturnal raptors in the last decade. Studies on urban raptors mainly focus on reproductive success, foraging pattern, and aggression in urban areas. Studies on top predatory bird species are essential while making management decisions, as these top predators might be responsible for keeping invasive faunal populations in check. For example, an increase in rodent populations on islands has led to the extinction of several island dwelling birds and other fauna [190]. Similar effects might affect bird populations in urban areas if proper management decisions are not taken at an appropriate time. Further, certain species are poorly represented in the research. Most of the studies that focus on species specific trait changes focus only on a few common species, such as great tits, Eurasian blackbirds, and house sparrows. Behavioral and physiological studies carried out on a couple of species might skew the literature in concluding effects of urbanization, either positive or negative and making generalizations. Caution should be taken that there is a lot of inter-species and intra-species variation and we need more studies looking at a variety of species and a combination of traits. For example, gulls seem to show extraordinary innovative ability around humans when compared to other urban birds. There is further scope to generate species specific databases in order to understand the effects of urbanization on diverse bird species and communities.

Urban areas provide a unique habitat in which to study community dynamics of birds. For example, in urban parks where there is a surge in activity during weekends, community composition of birds in these parks might be affected [78]. This could be very important, as, even though these are areas with good green cover, they might not be suitable nesting sites as park visitors might cause disturbance to nesting birds and might lead to abandoning the nest. On the other hand, these areas might be good areas to forage for fruits, seeds, and insects during the weekdays. An interesting hypothesis could be tested, looking at nesting success in the parks and outside the parks to actually see the effects of disturbance on bird communities and individual species.

5. Conclusions

The most significant trait changes that we identify have implications for urban avian diversity conservation, and they can be of use to park managers, citizen science groups, and urban planners. Omnivorous and cavity nesters have a better success in urban environments when compared to insectivores and ground nesting birds. Urban planners and park managers can maintain small patches of land that are enclosed to protect against common urban predators, such as feral dogs, cats, and rodents, in order to provide ground nesting birds that are especially endangered with refugia for roosting and nesting. Another important suggestion to bird enthusiasts and urban planners would be to include a variety of food items in bird feeders, as this might help birds with different diets to meet their nutrition requirements. Studies have shown that frugivores and granivores seem to do well in cities, as these birds feed on the seeds that are provided by people in bird feed. There has been evidence that, when artificial food is provided birds expand their ranges,

thus having a positive effect on bird populations [78]. If dried insects and nuts are included in the food, it might help insectivorous birds in the city. If bigger cavity nests are provided for birds, like owls and other larger species, then these species might bounce back in good numbers in the cities. Additionally, maintaining patches of native vegetation in urban habitats might be a great solution for supporting not only the bird species, but also insects and small mammal communities that can serve as a prey base to the birds. Along with patches of native vegetation, it is also crucial to conserve the local water bodies in cities, as these act as refuges for several migratory birds and local waders [46,191]. In the Mediterranean, it was observed that the natural waterbodies were key habitat for several species of owls [192]. Hence, the health of the lakes, ponds, and rivers is crucial for the survival of many urban species.

Species specific studies and detailed knowledge of local bird populations can greatly help in effective management measures, as we find substantial, documented variation in how birds of specific species respond to the pressures of urbanization. We hope for the long-term monitoring of bird populations while using a combination of detailed scientific research and citizen science initiatives, as demonstrated in the papers reviewed here, can help to bridge gaps in knowledge and benefit the future survival of a diverse range of birds in urban environments. To conclude, using a trait-based approach will be useful for understanding the impacts of urbanization on bird species. Understanding the role of traits with an understanding of urban changes will be most useful. In particular, we stress the need for further research on the traits that influence bird survival in tropical cities, as well as on individual species. A meta-analysis kind of an approach encompassing multiple traits together was out of scope for this study, as enough information on each trait is still not available. Some traits have enough literature, others have hardly a couple of studies. However, this review could act as a baseline for further research on urban wildlife and its ecology.

Supplementary Materials: The following are available online at www.mdpi.com/2073-445X/10/2/92/s1, Figure S1: List of journals which published the (>1) articles reviewed in the current study, Table S1: All traits considered for selecting the literature were distributed under five broad trait groups. In total, 32 sub-traits were considered for this study. The broad description of these sub-traits is given below, Table S2: List of publications reviewed for this study.

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