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Urbanisation and nest building in birds: a review of threats and opportunities

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Abstract

The world is urbanising rapidly, and it is predicted that by 2050, 66% of the global human population will be living in urban areas. Urbanisation is characterised by land-use changes such as increased residential housing, business development and transport infrastructure, resulting in habitat loss and fragmentation. Over the past two decades, interest has grown in how urbanisation influences fundamental aspects of avian biology such as life-history strategies, survival, breeding performance, behaviour and individual health. Here, we review current knowledge on how urbanisation influences the nesting biology of birds, which determines important fitness-associated processes such as nest predation and community assembly. We identify three major research areas: (i) nest sites of birds in urban areas, (ii) the composition of their nests, and (iii) how these aspects of their nesting biology influence their persistence (and therefore conservation efforts) in urban areas. We show that birds inhabiting urban areas nest in a wide variety of locations, some beneficial through exploitation of otherwise relatively empty avian ecological niches, but others detrimental when birds breed in ecological traps. We describe urban-associated changes in nesting materials such as plastic and cigarette butts, and discuss several functional hypotheses that propose the adaptive value and potential costs of this new nesting strategy. Urban areas provide a relatively new habitat in which to conserve birds, and we show that nestboxes and other artificial nest sites can be used successfully to conserve some, but not all, bird species. Finally, we identify those subject areas that warrant further research attention in the hope of advancing our understanding of the nesting biology of birds in urban areas.

Keywords Birds · Community · Conservation · Ecological trap · Nest design and site selection · Pollution

Introduction

We live in a world dominated by heavily human-impacted ecosystems such as warming oceans polluted by plastic and petrochemicals, and from which marine life has been over-harvested, forests either completely lost or heavily fragmented, rural areas farmed ever more intensively, and rapidly expanding urban areas (Ripple et al. 2017). Of all of

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these human-transformed environments, arguably it is urban areas that have been transformed most extensively (Johnson and Munshi-South 2017). By 2008, more than half of the world's human population was living in urban areas (United Nations 2014), with urbanisation continuing globally and rapidly (Seto et al. 2012). Accompanying this burgeoning human population in our towns and cities has been the emergence of the concept of the 'urban bird' (e.g., Evans et al. 2011; Marzluff 2014). Although such urban birds may be adapted to urban environments, the urbanisation process profoundly affects the majority of birds because it often involves the irreversible replacement of areas of natural and semi-natural rural habitats such as farmland and woodland with concreted areas of buildings and roads interspersed with gardens, parks and other green spaces (Forman 2014; Shanahan et al. 2014).

While urban birds face many challenges (reviewed in Marzluff 2017) that include exposure to novel predators (López-Flores et al. 2009), food sources (Jones and Reynolds 2008; Reynolds et al. 2017; Jones 2018), habitat types (Rodewald et al. 2013), thermal ranges (Davis et al. 2014a), and stressors such as noise (e.g., Fuller et al. 2007; Sierro et al. 2017), light (e.g., Kempenaers et al. 2010; Dominoni et al. 2013; Holveck et al. 2019) and air pollution (e.g., Isaksson 2015), their expansion and persistence in urban centres offers us many opportunities to understand processes of adaptation to urban living and the development of urban spaces as conservation areas for wildlife more generally. The responses of birds to extrinsic factors in the urban environment play out through processes such as synurbanisation (reviewed in Luniak 2004), biotic homogenisation (McKinney 2006; Galbraith et al. 2015; Ibáñez-Álamo et al. 2017a), and ecological traps (Dias 1996; Leston and Rodewald 2006; Sumasgutner et al. 2014a).

It is now rare to attend scientific mainstream ornithological meetings where there is not at least one session devoted to urban birds, and indeed, there are organisations such as the Urban Wildlife Working Group (<http://urbanwildlifegroup.org/>) that host entire annual conferences devoted to public awareness and management of urban wildlife, including birds. Increasing ornithological interest in urban birds, and especially in their behaviour and ecology, has resulted in the publication of numerous books in this subject area (e.g., Bird et al. 1996; Marzluff et al. 2001; Lepczyk and Warren 2012; Gil and Brumm 2013; Marzluff 2014; Murgui and Hedblom 2017; Jones 2018). Despite this, Reynolds and Deeming (2015) argued that compared with our knowledge of avian life history, behavioural ecology, distribution and abundance, our understanding of the nesting biology of birds is rather limited. This is particularly striking within the urban context. Birkhead (2015) singled out the nesting biology of birds as being fertile ground for future research, even in meeting the primary fundamental scientific aim of

obtaining first nest descriptions of most (i.e., an estimated 55%; W. Jetz, pers comm) of the world's avifauna (Reynolds and Deeming 2015). It is shocking that we lack such basic information about extant bird species; such nest descriptions will inevitably promote a greater understanding of broader disciplines such as ecology and evolution of birds.

Given that birds invest considerable time and energy in nest building and maintenance (Hansell 2000; Stanley 2002), it is surprising that the nesting biology of birds has been rather neglected as a research focus compared to other aspects of their breeding biology (Deeming and Reynolds 2015a). We now need to go beyond studies that describe how the breeding performance of birds varies with urbanisation (e.g., Tremblay et al. 2003; Partecke et al. 2004; Hedblom and Söderström 2012). As part of this, a focus on investments of time and energy in the location of suitable nest sites and the subsequent construction and maintenance of nest structures would greatly enhance our understanding of the life history and ecology of urban birds (Deeming and Reynolds 2015b). Discussions are currently under way between the authors of this paper and the wider ornithological community about how we can carry out concerted, complementary and meaningful research that is performed in a standardised manner on urban birds at a global scale within urban study sites. Therefore, we have taken this opportunity to write about just one subject area (of many) that we feel has the potential to bring field ornithologists together, whether they are professional or citizen scientists (Greenwood 2007; Dickinson and Bonney 2012; Cooper 2017).

We have chosen to direct the focus of this paper to three different subject areas related to the nesting biology of birds in urban areas. First, we address where urban birds nest, which is essential in making assessments about nest site availability in cities (Kark et al. 2007), allowing subsequent estimation of important measures such as breeding density of study species (Šálek et al. 2015), and heterospecific and conspecific competition (Evans et al. 2009a, 2009b). Secondly, we explore the form of urban nest design allowing quantification of investment in nest construction and maintenance by breeding birds (Mainwaring et al. 2014a) as well as potential relationships between the structure and composition of nests and their fitness-associated consequences for urban birds (e.g., Reid et al. 2002). Thirdly, we discuss to what extent the nesting biology of target species can inform conservation actions and ultimately policy (Collar and Butchart 2014; Deeming and Jarrett 2015). Conserving birds in urban areas may seem to be a low priority for conservationists, given that they inhabit a highly artificial and generally biodiversity-poor environment. However, numerous studies have shown that birds inhabiting urban areas comprise almost all of the interactions that most people living in urban areas have, and that such interactions provide psychological benefits to those people (reviewed in Cox

et al. 2017). Such interactions also allow human–wildlife engagement to mediate opportunities for raising conservation awareness. Furthermore, some threatened species have important populations in urban areas (e.g., UK gulls [Laridae]—Raven and Coulson 1997; German Common Swifts [*Apus apus*]—Schaub et al. 2015), and so we consider that many urban birds are of conservation concern. Finally, we identify key areas for future research that we hope will place the nesting biology of birds at the core of our understanding of how avian species adapt to urban life across the globe (Kark et al. 2007; Croci et al. 2008; Sol et al. 2014).

Urban nest sites

In this section, we consider how the availability of nest sites in native and non-native vegetation, houses, uninhabited buildings, a variety of anthropogenic structures such as metal pipes and bridges, and provision of nestboxes influence birds nesting in urban areas worldwide (summarised in Table 1; Fig. 1). Native trees and flowering plants have been progressively removed from urban areas because they are considered ‘weeds’; they are replaced with non-native vegetation (Marzluff et al. 2001; Reale and Blair 2005; Forman 2014). Illustratively, an average of 2.4 native plant species were lost annually over a period of seven decades in cities in Indiana in the USA, whilst over the same period 1.4 species of non-native plant species were introduced per annum (Dolan et al. 2011). Loss of native vegetation can present problems to breeding passerines whose reproductive success is often higher in native, as opposed to non-native, vegetation (Borgmann and Rodewald 2004; Rodewald et al. 2010; but see Meyer et al. 2015). Despite birds often having higher levels of breeding success in native vegetation, Vincze et al. (2017) used a

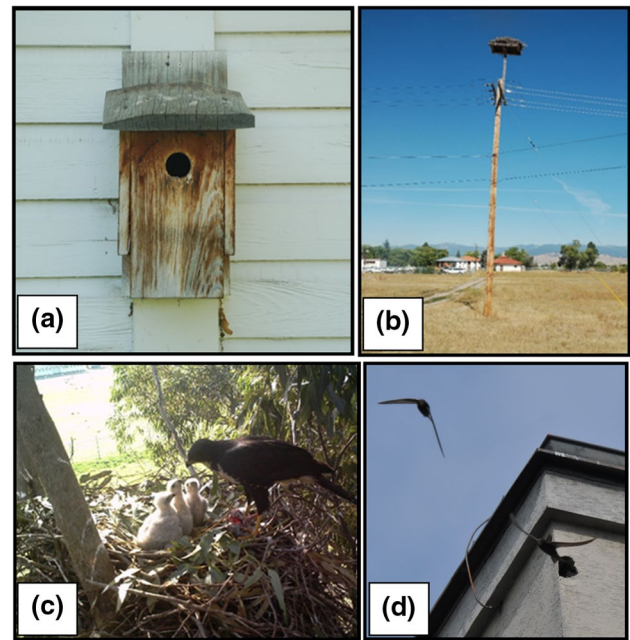


Fig. 1 Nest sites of birds in urban areas include: **a** a nestbox for passerines; **b** an artificial nest platform for raptors such as Ospreys (*Pandion haliaetus*) (Photo: Mark Mainwaring); **c** an open nest in non-native vegetation such as that of Black Sparrowhawks (*Accipiter melanoleucus*) (Photo: Petra Sumasgutner); and **d** a nesting hole of a Common Swift (*Apus apus*) (Photo: Ferdinand Schmeller/MA22)

meta-analysis to show that the detection of birds’ nests by predators generally declined with increasing urbanisation. How this is related to the replacement of native with non-native vegetation remains unclear.

Many studies of passerines report that nest sites in non-native vegetation act as ecological traps (e.g., Borgmann and Rodewald 2004; Rodewald et al. 2010). This is thought to be because breeding passerines forage close to their nest

Table 1 A list of the main categories of nest substrates used by urban birds and the main advantages and disadvantages to birds nesting in them

Nest substrate	Advantages	Disadvantages
Native vegetation	Likely to be optimal breeding sites, as birds are well adapted over evolutionary time	Majority of such sites have been lost through increasing intensity of urbanisation
Non-native vegetation	Most commonly available breeding habitat type and supports insect prey base for prolonged periods compared with native vegetation	Generally supports a reduced insect prey biomass compared with native vegetation. May therefore act as an ecological trap
Houses	Widely available nest site for cavity nesters at sites where nesting opportunities are otherwise limited	Householders may be opposed to birds using their homes as breeding sites
Uninhabited buildings	Safe (undisturbed) nest sites often in areas where prey are abundant	May be ecological traps as evidenced by breeding birds paying fitness costs
Anthropogenic (non-residential) structures	Provision of nest sites where otherwise they are in limited supply	May be ecological traps due to their only temporary availability
Nestboxes	Nest sites in public parks, and public and private gardens suffering lower rates of predation compared with natural sites	May be ecological traps due to birds breeding at high density but under conditions of intense competition for sometimes limited food

sites, where non-native plants support a lower food base for nestlings than do native plants (Ortega et al. 2006). These urban-associated changes in vegetation could also partially explain why urban areas fledge fewer offspring per breeding attempt than rural areas, although annual productivity is generally higher due to earlier and/or longer breeding seasons which allow more breeding attempts per season (Chamberlain et al. 2009). Other studies, however, have reported that birds nesting in non-native vegetation have at least equal levels of breeding success to conspecifics in native vegetation (e.g., Schlossberg and King 2010; Meyer et al. 2015). Such equivocal findings reflect the conclusions of the most recent review in this subject area by Stinson and Pejchar (2018). They reviewed 32 studies examining 133 songbird species' responses to nesting in non-native vegetation. Although 35% of studies found some evidence for non-native plants acting as ecological traps through negative impacts on the birds' productivity, fledgling and adult survival, nestling condition and brood parasitism rates, 31% of studies found positive impacts on the same parameters.

Inhabited buildings such as houses or blocks of flats commonly provide nest sites for species such as Common Swifts (Fig. 1d), Common Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*) that nest in the eaves of houses (Mainwaring 2015), although their nest sites have been the subject of little research. This is somewhat surprising given that such species are urban specialists that overwhelmingly breed at unnatural nest sites, which means, in turn, that they are likely to have wider geographic ranges and larger population sizes as a result of the expansion of urban areas (De Laet and Summers-Smith 2007). Inhabited buildings also provide nest sites for waders such as Eurasian Oystercatchers (*Haematopus ostralegus*) (Munro 1984) and gulls that nest on rooftops (Vermeer et al. 1988; Raven and Coulson 1997; Soldatini et al. 2008). The widespread availability of nest sites on rooftops has facilitated dramatic population increases in urban gulls over the past few decades (Soldatini et al. 2008). Much has been made of this by many local authorities and the media, because the growing number of urban gulls increases the likelihood of conflict between birds and humans, with associated public health impacts. For example, there is a significant chance of faecal contamination of urban water supplies (Hatch 1996) and of pathogens such as bacteria and viruses being spread. Studies have suggested that European Herring Gulls (*Larus argentatus*) act as vectors in outbreaks of *Salmonella montevideo* in sheep (*Ovis aries*) and cattle (*Bos taurus*) in Scotland (Coulson et al. 1983) and that Olrog's Gulls (*Larus atlanticus*) and Kelp Gulls (*Larus dominicanus*) act as vectors for a range of zoonotic pathogens in Argentina (La Sala et al. 2013). Nesting close to houses may also induce behavioural changes in birds. For example, Møller and Díaz (2018) found that birds

nesting closer to inhabited buildings reduced their anti-predator behaviours because they were exposed to fewer predators than conspecifics nesting further away from houses.

A range of bird species nest in large numbers either on or in uninhabited buildings in urban areas that include factories, shops and abandoned residential buildings. For example, more than 500 pairs of Glaucous-winged Gulls (*Larus glaucescens*) nested on roofs along the waterfront in Vancouver, BC, Canada (Vermeer et al. 1988), and 11,047 pairs of European Herring Gulls and 2544 pairs of Lesser Black-backed Gulls (*Larus fuscus*) nested on buildings and other man-made structures in the UK (Raven and Coulson 1997). Uninhabited buildings in cities appear to provide breeding opportunities that are as good for urban gulls as rural habitats, with populations exhibiting equivalent breeding performance (Soldatini et al. 2008). Even though birds such as gulls and other urban species widely use uninhabited buildings as nest sites, they also nest in rural areas and are therefore not completely reliant upon uninhabited buildings to provide nesting opportunities. In contrast, urban specialists such as Common Swifts and House Sparrows nest almost exclusively on uninhabited buildings in urban areas (De Laet and Summers-Smith 2007), which means that their populations are likely to be closely tied to the availability of these structures. Therefore, we need to know much more about the reliance of such urban specialists upon uninhabited buildings. In summary, nest sites on uninhabited buildings may be widely available, but additional work is needed to determine how advantageous they are for breeding birds compared with other urban sites.

Birds also nest either on or in a variety of anthropogenic structures such as bridges and metal pipes (Mainwaring 2015). Bridges over both water and roads provide safe breeding sites for birds in locations where nest sites may well be limited, although traffic does pose a risk for birds nesting over roads, because they collide with cars (Brown and Brown 2013). Whilst the majority of studies simply state that birds use such structures as nest sites, few have quantified their importance relative to other nest substrates. A notable exception was a study by Lesiński (2000) that examined nest sites of a range of hole-nesting passerine species in a suburb of Warsaw, Poland. It was found that many birds were nesting inside vertical pipes of fences, where approximately 80% of the local Great Tit (*Parus major*) population were estimated to be breeding. While for some avian taxa, therefore, pipes and other anthropogenic structures provide unlikely breeding opportunities in locations where nest sites may be in short supply, others such as pigeons and doves (Columbiformes) are sometimes deterred from exploiting such opportunities through the placement of obstructing metal pins that prevent them from alighting on window ledges, under bridges and on other similar structures. These structures often only offer ephemeral nesting opportunities

to birds because either they are temporary supporting structures or they are the first piece of infrastructure that falls into disrepair, sometimes leading to their removal because of public safety concerns. Therefore, anthropogenic structures may also act as ecological traps by attracting birds to breed in locations that ultimately reduce their fitness (Schlaepfer et al. 2002).

Nestboxes, artificial platforms and even artificial burrows are widely provided for birds such as passerines (Passeriformes) (e.g., Remacha and Delgado 2009; Schaub et al. 2015; Reynolds et al. 2016; Duckworth et al. 2017; Lambrechts et al. 2017; Fig. 1a), storks (Ciconiiformes) (e.g., Tryjanowski et al. 2009), raptors (Falconiformes) (e.g., Postupalsky and Stackpole 1974; Tigner et al. 1996; Fig. 1b), owls (Strigiformes) (e.g., Smith et al. 2005) and swifts (Apodiformes) (e.g., Schaub et al. 2015) within urban landscapes. Whilst at first sight nestboxes provided by individual householders may appear to provide few nesting opportunities for urban birds, nestboxes can be highly abundant in some urban areas. For example, it was estimated that there were 45,500 nestboxes in the city of Sheffield in northern England (Gaston et al. 2005), and Davies et al. (2009) estimated that there were at least 4.7 million nestboxes in gardens in Great Britain. These studies indicate that nestboxes can provide abundant nest sites in some urban areas in some countries (e.g., the UK, the USA), where they certainly address shortfalls in nest site availability. However, nestboxes might be advantageous for birds only when located in areas of high food abundance, and otherwise can act as an ecological trap (Demeyrier et al. 2016). We also acknowledge that nestboxes are not provided to birds globally.

Within urban areas, birds use a wide variety of nest sites that offer benefits but also detriments to birds occupying them, as summarised in Table 1. There is, however, a general trend for the variety of potential nest sites to decline as the urbanisation process advances, but with some nest sites that are either in or on houses, for example, increasing in availability to breeding birds (Rao and Koli 2017). Although it is unlikely that a reduction in the availability of nest sites has been responsible for changes in bird assemblages inhabiting urban areas (Oliveira Hagen et al. 2017), homogeneity of nest site form is reflected in an overall decline in species richness in urban areas; some species, of course, may exploit more breeding opportunities as a result (Ibáñez-Álamo et al. 2017a). The limitations of avian breeding potential in cities caused by the scarcity of nest sites can however be addressed by the provision of nestboxes, artificial platforms and native vegetation. Private citizens and municipal employees can play fundamental roles in increasing nest site availability to birds prospecting in spaces that they either own or manage.

Nest design and urbanisation

In addition to the changes in nest sites described above, urbanisation can affect different aspects of nest design of birds. In this context, nest composition has received increasing attention recently (Table 2). Several studies have highlighted a change in nesting materials along an urbanisation gradient (e.g., Wang et al. 2009; Radhamany et al. 2016; Reynolds et al. 2016), while others did not find such effects (e.g., Townsend and Barker 2014; Hanmer et al. 2017), suggesting that nest design may exhibit species-specific or even city-specific differences. It is also possible that the latter studies failed to find changes in nest composition because they considered too small a variation in human activities along their urbanisation gradient by including urban and intensively agricultural areas but not natural areas for comparisons. The main changes in nest composition are associated with an increased use of anthropogenic nesting materials and a reduction in natural materials, especially native plants (Wang et al. 2009; Radhamany et al. 2016). Increased use of other components such as feathers as nesting materials have also been described (e.g., Reynolds et al. 2016).

Several hypotheses have been proposed to explain these changes in nest composition. Some authors argue that the main cause is the reduction in native plants (and plant material in general) in addition to the higher availability of other anthropogenic materials (e.g., plastics) in urban areas (Wang et al. 2009). This ‘availability hypothesis’ assumes that birds simply select the materials most widely available, with no adaptive value of such changes, and is supported by the fact that nest composition varies according to the local availability of nesting materials (Wimberger 1984), including those that are anthropogenic (Jagiello et al. 2018). Interestingly, Black-faced Spoonbills (*Platalea minor*) reduced anthropogenic materials in their nests when supplied with natural elements in their nest surroundings (Lee et al. 2015), suggesting that cities might provide suboptimal nesting materials for birds. The abundance of certain plants (e.g., pines [*Pinus* spp.]) in the city of Montpellier, France is also linked to the use of pine needles by urban Great Tits, a nesting material not used by populations in non-urban locations (Lambrechts et al. 2017), supporting this hypothesis as well. A second idea (the ‘age hypothesis’) would suggest that urban-associated changes in nest composition might be due to cities being inhabited by older birds (e.g., Evans et al. 2009b; Ibáñez-Álamo et al. 2018) and the increasing use of anthropogenic nesting materials with age in some species (Sergio et al. 2011; Jagiello et al. 2018). The causes of this association between age of breeder and use of anthropogenic nesting materials are unclear, but it is likely that previous experience in the habitat plays a role. This supports predictions from the age hypothesis that urban birds are older due

Table 2 Details of studies (by continent) that have investigated nest design of urban bird species

Continent	Species name	Study type	Part of nest studied	Anthropogenic nesting material? (Y–Yes; N–No)	Nest type	Nest site	Source
Asia	Baya Weaver (<i>Ploceus philippinus</i>)	Observational	No distinction	N	Dome	Native vegetation	Sohi and Kler 2017
	Common Myna (<i>Acridotheres tristis</i>)	Observational	No distinction	Y	Cavity	Native vegetation, houses, anthropogenic structures	Sohi and Kler 2017
	Common Pigeon (<i>Columba livia</i>)	Observational	No distinction	Y	Open	Houses, uninhabited buildings, anthropogenic structures	Sohi and Kler 2017
	Common Swift (<i>Apus apus</i>)	Observational	No distinction	N	Hole	Houses	Sohi and Kler 2017
	Cattle Egret (<i>Bubulcus ibis</i>)	Observational	No distinction	Y	Open	Native vegetation	Sohi and Kler 2017
	Eurasian Collared Dove (<i>Streptopelia decaocto</i>)	Observational	No distinction	Y	Open	Native vegetation, houses	Sohi and Kler 2017
	House Crow (<i>Corvus splendens</i>)	Observational	No distinction	Y	Open	Nestbox	Sohi and Kler 2017
	House Sparrow (<i>Passer domesticus</i>)	Observational	Lining	Y	Hole	Not specified	Radhamany et al. 2016
	House Sparrow	Observational	No distinction	Y	Hole	Not specified	Sohi and Kler 2017
	Light-vented Bulbul (<i>Pycnonotus sinensis</i>)	Observational	No distinction	Y	Open	Not specified	Wang et al. 2009
	Pied Myna (<i>Sturnus contra</i>)	Observational	No distinction	Y	Dome	Native vegetation, anthropogenic structures	Sohi and Kler 2017
	Purple Sunbird (<i>Cinnyris asiaticus</i>)	Observational	No distinction	Y	Dome	Native vegetation	Sohi and Kler 2017
	Red-vented Bulbul (<i>Pycnonotus cafer</i>)	Observational	No distinction	Y	Open	Native vegetation	Sohi and Kler 2017
	Red-wattled Lapwing (<i>Vanellus indicus</i>)	Observational	No distinction	N	Open	Ground	Sohi and Kler 2017
	Rose-ringed Parakeet (<i>Psittacula krameri</i>)	Observational	No distinction	Not specified	Hole	Native vegetation	Sohi and Kler 2017
	Scaly-breasted Munia (<i>Lonchura punctulata</i>)	Observational	No distinction	Y	Dome	Native vegetation	Sohi and Kler 2017
Europe	Wire-tailed Swallow (<i>Hirundo smithii</i>)	Observational	No distinction	N	Hole	Houses	Sohi and Kler 2017
	Blue Tit (<i>Cyanistes caeruleus</i>)	Observational	Nest base and lining	Y	Hole	Nestbox	Reynolds et al. 2016
	Blue Tit	Observational	No distinction	Y	Hole	Nestbox	Hanmer et al. 2017

Table 2 (continued)

Continent	Species name	Study type	Part of nest studied	Anthropogenic nesting material? (Y–Yes; N–No)	Nest type	Nest site	Source
North America	Great Tit (<i>Parus major</i>)	Observational	No distinction	Y	Hole	Nestbox	Hanmer et al. 2017
	Great Tit	Observational	No distinction	N	Hole	Nestbox	Lambrechts et al. 2017
	American Crow (<i>Corvus brachyrhynchos</i>)	Observational	No distinction	Y	Open	Not specified	Townsend and Barker 2014
	House Finch (<i>Haemorrhous mexicanus</i>)	Observational	Lining	Y	Open	Not specified	Suárez-Rodríguez et al. 2013, 2017
	House Finch	Experimental	Lining	Y	Open	Not specified	Suárez-Rodríguez and Macías García 2014, 2017
	House Sparrow	Observational	Lining	Y	Hole	Not specified	Suárez-Rodríguez et al. 2013, 2017

to their higher survival rates compared to conspecifics in rural areas, as opposed to older birds dispersing to cities from natural or rural habitats, although these possibilities remain to be tested experimentally. The availability and age hypotheses assume that anthropogenic materials are used because of their resemblance to naturally occurring nesting materials (Antczak et al. 2010; Townsend and Barker 2014; Biddle et al. 2018), although there has been no direct test of this assumption. Additionally, the ‘new location hypothesis’ proposes that such changes in nest composition are driven by changes imposed by the locations of nest sites in new areas (Reynolds et al. 2016). In contrast to predictions from the availability hypothesis, urban birds would change their nesting materials as a consequence of using alternative (new) nest sites that impose different requirements. Some authors have raised concerns over the potential bias associated with the use of nestboxes when investigating factors such as nest ectoparasite exposure, anti-predator defences and constraining size limitations of the nest substrate (Wesołowski and Stanska 2001; Wesołowski 2011). The comprehensive use of nestboxes to study birds in many cities compared with studies of birds in natural nesting habitats, and the potential link between some of these nestbox traits and nest composition, lend support to the new location hypothesis. Other urban-associated changes in nest sites like those undertaken by Common Blackbirds (*Turdus merula*) nesting on window canopies or balcony frames rather than in vegetation in China (Wang et al. 2015) and Europe (JD Ibáñez-Álamo pers obs), or by Eurasian Magpies (*Pica pica*) nesting on chimneys and roofs instead of trees in the city of Hangzhou, China (Wang et al. 2008), might also indicate that modifications to nest composition that allow for secure attachment of nests to substrate are not insurmountable for urban birds.

Finally, the ‘adaptive hypothesis’ assumes that changes to nest design are driven by their adaptive value. The strongest support for this hypothesis is provided by research demonstrating that some urban species actively use smoked cigarette butts for self-medication. Through a series of manipulative and observational studies, researchers were able to prove that the use of cigarette butts by a common Mexican urban species, the House Finch (*Haemorrhous mexicanus*), fulfils all three of the characteristics of self-medication behaviour as described by Clayton and Wolfe (1993): (1) they are detrimental to parasites (Suárez-Rodríguez et al. 2013), (2) they are actively selected by birds (Suárez-Rodríguez and Macías García 2017), and (3) they increase their fledging success (Suárez-Rodríguez and Macías García 2014). The use of cigarette butts is not just restricted to House Finches in Mexico (Suárez-Rodríguez and Macías García 2017), and has been found in other species such as House Sparrows in North America (Suárez-Rodríguez et al. 2013, 2017) and Asia (Radhamany et al. 2016), suggesting that it might be a general behavioural innovation for urban-adapted species. In contrast, Blue Tits (*Cyanistes caeruleus*), a species that does not use cigarette butts as nest constituents, in the town of Reading, UK using more anthropogenic nesting material had larger numbers of fleas (Siphonaptera) within their nest contents (Hanmer et al. 2017). The authors argue that this is caused by a reduction in the diversity of nest-dwelling arthropods (including potential competitors and predators of flea larvae). Overall, these studies suggest that the potential adaptive value of changes in nest composition might depend on the relative availability and properties (e.g., antimicrobial) of anthropogenic nesting materials within breeding habitats.

The anti-parasitic function is not the only adaptive function that can be performed by anthropogenic nesting materials used by birds breeding in cities (Mainwaring et al. 2014b). Some of this can perform a signalling function. For example, plastics in nests of Black Kites (*Milvus migrans*) may be involved in intraspecific signalling, as they can provide information about the nest owner's 'quality' (Sergio et al. 2011). Anthropogenic nesting materials are also used in sexual selection by bow-erbirds (Ptilonorhynchidae) (e.g., Borgia 1985). Interestingly, the visual component of cigarette butts does not appear to perform this function in Song Thrushes (*Turdus philomelos*), although it might play a part as an olfactory signalling component (Igic et al. 2009). However, these ideas about signalling remain untested in urban birds and require further investigation before associating it with the urbanisation process. The only link between this signalling function and urbanisation so far has been made to explain changes in the number of feathers along an urbanisation gradient in Blue Tit nests from the city of Birmingham, UK (Reynolds et al. 2016). This is based on the idea that feathers may signal intrusions into nests by competitors (Mainwaring et al. 2016) and that density of birds can change as a result of urbanisation (Evans 2010). Although only suggestive, such changes in nest design might also occur in response to changes in sexual selection (Sanz and García-Navas 2011) or microbial loads (Peralta-Sánchez et al. 2010; Ruiz-Castellano et al. 2016) along the urbanisation gradient, and therefore will require further studies before reaching firm conclusions. Changes in the thermal properties of nests could also explain variation in nest composition along the urbanisation gradient if, for example, anthropogenic and natural materials have different insulating properties. Cities contain urban heat islands where ambient temperature can be a few degrees Celsius higher than in non-urban areas (Oke 1982; Forman 2014). However, this thermal urban phenomenon has not been explored in the context of nest design, although the improvement of nest microclimate has been proposed to explain the use of certain anthropogenic materials as nest components (Igic et al. 2009). Finally, nesting materials can also play an important role in avoiding nest predation (Mainwaring et al. 2015). In fact, it has also been suggested that some anthropogenic materials such as cigarette butts might have anti-predatory functions, potentially deterring odour-driven predators (Igic et al. 2009), but this idea has not been investigated to date.

Despite the potential benefits, changes in nest composition associated with urbanisation might translate into costs incurred by the avian constructor. The use of cigarette butts, for example, imposed costs on both nestlings and adult birds that experienced higher genotoxic damage, possibly because of the many toxic substances contained

in cigarettes (Suárez-Rodríguez and Macías García 2014; Suárez-Rodríguez et al. 2017). Interestingly, this damage occurred only in the sex(es) that participated in nest building, indicating that costs incurred may be sex-specific according to parental roles (Suárez-Rodríguez et al. 2017). Whether this damage implies long-term or even fertility costs is not known, but it will be crucial to identify the net fitness balance of the use of cigarette butts and potentially other novel nesting materials in the urban environment. Other studies have demonstrated that anthropogenic nesting materials (e.g., plastic twine, fishing line or metal pieces) in the nests of several species are associated with an increased frequency of nestling deaths from entanglement, strangulation and other injuries (Blem et al. 2002; Parker and Blomme 2007; Antczak et al. 2010; Henry et al. 2011; Townsend and Barker 2014).

Within a cost–benefit context, we believe that mechanistic studies offer some of the best ways to understand trade-offs faced by breeding urban birds. This is clearly exemplified by the studies of Mexican House Finches which found that cigarette butts promoted an immuno-enhancement effect and mass gain in chicks, but they also induced erythrocyte genotoxicity in nestlings and adults (Suárez-Rodríguez and Macías García 2014; Suárez-Rodríguez et al. 2017). Such research provides new insights into the non-lethal effects of anthropogenic materials and potentially explains why urban areas might be ecological traps for certain avian species (Dias 1996; Leston and Rodewald 2006; Sumasgutner et al. 2014a). Similarly, they could offer much needed information to understand the positive and negative effects of urban-associated changes in nest composition. While clearly anthropogenic materials such as cigarette butts assist ectoparasite control in nests, we still lack a deep understanding of how they reduce ectoparasite loads of nests, promote changes in the arthropod community of nests and improve nestling health (Suárez-Rodríguez et al. 2013; Hanmer et al. 2017).

Nest structures are another important variable in nest design (Deeming and Reynolds 2015). According to Hansell (2000), there are four main parts/structures in nests: attachment, outer (decorative) layer, structural layer and lining. Apart from the study of Radhamany et al. (2016), investigations of how urban environments impact nest design either quantify materials without distinction (e.g., Wang et al. 2009; Sohi and Kler 2017) or are focused exclusively on changes to the nest lining (e.g., Suárez-Rodríguez et al. 2013), paying very little attention to other structures. This is probably a consequence of anthropogenic nesting materials being more commonly used as lining material, although some taxa such as thrushes (Turdidae) seem to use them as structural material as well (Biddle et al. 2016). Many turdids are among the most common urban bird species (e.g., Wang et al. 2015; Ibáñez-Álamo et al. 2017b, 2018), which makes them excellent candidate subjects for further study.

Previous studies provide mixed support for the variation in nest size and mass in association with urbanisation. On the one hand, several authors found no variation in nest mass or size along an urbanisation gradient for Blue or Great Tits in different European cities (Gładalski et al. 2016; Reynolds et al. 2016; Lambrechts et al. 2017). On the other hand, Hanmer et al. (2017) found that Blue Tits, but not Great Tits, in the same English town had lighter nests in more urbanised areas. This could be explained in a thermal context, as several studies have found geographical variation in nest size/mass that has been attributed to variations in ambient temperature (Deeming et al. 2012; Mainwaring et al. 2012, 2014a; Biddle et al. 2016). Other constraints such as the lack of appropriate materials or new nest locations could also influence nest size and mass. Overall, this topic is clearly understudied, and future investigations should try to test these hypotheses by studying different bird species (e.g., open nesters) and in different geographical areas (e.g., high-latitude or tropical areas).

Urban nesting biology and conservation

Urbanisation is currently considered a major global challenge, not least to nature conservation (Miller and Hobbs 2002; McKinney 2006; Ibáñez-Álamo et al. 2017a). Worldwide, urban areas heavily influence the ecology of animal species through habitat loss, increased fragmentation and pollution, or communities that often contain more invasive species (Alberti et al. 2003; Grimm et al. 2008). Nevertheless, the proximity of humans to birds creates valuable opportunities for public engagement and urban conservation (Marzluff 2014). Such engagement could focus on cavity-nesting species, as this is a nesting trait that appears to be shared by most successful breeders in the urban environment (Chace and Walsh 2006; Kark et al. 2007). Therefore, there is a clear opportunity to use nestboxes specifically as a conservation tool. The availability of different kinds of nestboxes may increase the colonisation of urban parks by a great variety of cavity-nesters, including threatened species (Jokimäki 1999; Jokimäki et al. 2018). Nestboxes increase breeding opportunities for urban birds, because there are fewer natural cavities or hollows in trees in urban areas than in continuous woodlands (Davis et al. 2014b); they ensure that nest sites are available in areas where they would otherwise be limiting (Schaub et al. 2015). They can, however, also be disadvantageous by acting as ecological traps (Demeyrier et al. 2016) or by being occupied by a variety of invasive species of birds (Garrock et al. 2013; Bender et al. 2016) and mammals (Harper et al. 2005). For example, although the number of Peregrine Falcon (*Falco peregrinus*) pairs increased in Cape Town, South Africa at the same time as nestboxes were provided, it was immigration that

drove the population increases (Altwegg et al. 2014), which illustrates more broadly that nestboxes are only useful when nest sites are in limited supply. In another study in Madrid, Spain, nestboxes were utilised not only by parids but also by other species. Tree Sparrows (*Passer montanus*) took over the nestboxes, constructing nests that filled the entire box, thereby rendering them inaccessible to other species looking to use them for future breeding attempts (Fernández-Juricic and Jokimäki 2001).

Despite many negative effects of urbanisation on wildlife, several threatened bird species, including critically endangered ones, inhabit urban core areas; they include White-rumped Vultures (*Gyps bengalensis*) in Kolkata, India, Orange-bellied Parrots (*Neophema chrysogaster*) in Melbourne, Australia, Spoon-billed Sandpipers (*Eurynorhynchus pygmeus*) and Christmas Frigatebirds (*Fregata andrewsi*) in Singapore, and Balearic Shearwaters (*Puffinus mauretanicus*) in Valencia, Spain (Aronson et al. 2014). Jokimäki et al. (2018) concluded that within European cities, most threatened species commonly nest in cavities, including House Sparrows, Common Swifts and House Martins (*Delichon urbica*). If a species is able to exploit opportunities such as holes and cavities in buildings for nesting while tolerating human presence, this may facilitate population growth and establishment in the novel breeding niches in cities (see review by Tomiałojć 2016). Authors including Schaub et al. (2015) suggest that modern building design should accommodate the breeding requirements of cavity-nesting species. Additionally, creation and management of urban green spaces should include retention of old trees, providing cavities and/or provision of nestboxes to support breeding attempts of threatened, cavity-nesting species such as Orange-bellied Parrots in Australia (Loyn et al. 1986). While such conclusions promote conservation of urban birds, they result in other fundamental considerations such as whether human-made nest structures should be designed to exclude potential predators, and who should be responsible for their maintenance to prevent damage to buildings or injuries to the general public.

The challenges for avian conservation in cities broadly fall into two categories: (i) the amount of human interference in an already altered ecosystem, and (ii) emerging human–wildlife conflicts often encountered in urban environments where humans and other species live in close proximity to each other. As one of the most dramatically transformed, fragmented and highly disturbed habitats on Earth, species richness in urban areas is lower than in nearby natural areas (e.g., McKinney 2008; Ibáñez-Álamo et al. 2017a), and this is reflected in simplified food webs and a greater influence of bottom-up processes (Faeth et al. 2005). Many of these urban habitat features have implications for nesting birds and offer opportunities for management to improve productivity and survival. For example,

habitat fragmentation increases the amount of edge habitat (Murcia 1995). This edge-related gradient systematically alters abiotic variables near the edge, but also affects biotic interactions (Fagan et al. 1999). The edge functions as a dispersal barrier or filter and can influence mortality or generate novel interactions (Fagan et al. 1999), as seen in birds' nests that are more likely to be parasitised by cowbirds (*Molothrus* spp.) when they are located near a habitat edge (Lloyd et al. 2005). Providing nesting habitat or nest sites in larger urban green patches with proportionally reduced edge habitat could reduce the frequency of brood parasitism. Another example is the Spotted Towhee (*Pipilo maculatus*) that prefers forest edges near residential areas in Portland, Oregon, USA, where they fledge more young compared to birds selecting nest sites in the forest interior (Shipley et al. 2013). However, nestling mortality is lower in the forest interior, owing to high predation by Domestic Cats (*Felis catus*) and Western Screech Owls (*Megascops kennicottii*) at the forest edge.

Another global characteristic of urban areas is an increase in anthropogenic disturbance and pollution that can lead to modified nest placement and creation of ecological traps as a result. For example, Black-billed Magpies (*Pica hudsonia*) (Wang et al. 2008) and Eurasian Magpies (Jerzak 2001) nest significantly higher above the ground with urbanisation intensity. Another example is provided by the Syrian Woodpecker (*Dendrocopos syriacus*) that prefers areas where pollution weakens trees and increases the abundance of bark-dwelling insects inhabiting them, but where birds may be negatively impacted by air pollution itself, reducing their body condition (Ciach and Frohlich 2013). Of course, such considerations will ultimately shape conservation measures such as the placement of artificial nest sites if so desired.

Urbanisation also acts as a filter which excludes some species and changes the composition of avian communities through novel and rapid evolutionary forces (Shanahan et al. 2014). The filtering mechanism that results in avian communities we observe in urban environments is not well understood, but at its heart is also the human component itself. For example, we facilitate the breeding of many bird species in urban environments by intentionally providing supplementary food or artificial nest sites (Robb et al. 2008; Davies et al. 2009). As part of such interventions, we need to make conscious decisions about which species we are targeting (and looking to deter) and where to provide such support. Our provision of nesting habitat or artificial nest sites not only favours a limited number of species (e.g., cavity nesters that use nestboxes), but also favours species that are considered charismatic by citizens, such as small passerines and falcons (Falconidae). Contrary to this, we install deterrents such as metal pins to prevent some less favoured species such as corvids (Corvidae), pigeons and doves from nesting or even alighting on urban infrastructure. Understanding

which urban species are encouraged or discouraged by our activities is fundamental before we promote conservation initiatives that require significant inputs (e.g., time, money, energy) from citizens (Toft 2014). This strikes at the heart of the emerging discipline of ethno-ornithology (Tidemann and Gosler 2010) that examines human–bird interactions through integration of traditional (TEK) and scientific ecological knowledge (SEK) bases (Cocker and Tipling 2013).

Human–wildlife conflicts emerge globally (Redpath et al. 2013) wherever humans and wildlife compete for resources, and often require wildlife management. Wildlife management is primarily a human response to reduce or eliminate causes of economic or social damage caused by wildlife (Treves et al. 2006), and conservation goals are becoming an important part of such management (Redpath et al. 2013). Urban birds are no exception. For example, urban areas are like all transformed ecosystems vulnerable to invasive species (Godefroid and Ricotta 2018). Unlike temperate areas, there is a lack of data on what kinds of decorative ornamental plants are being used in urban green areas in tropical countries (Müller et al. 2013). Native bird species diversity has been shown to decline with an increase in exotic plant species in Delhi, India (Khera et al. 2009). However, there are examples where birds profit from alien plants in urban green space, as seen in the recent colonisation of Cape Town, South Africa by Black Sparrowhawks (*Accipiter melanoleucus*) (Martin et al. 2014), or the Crowned Eagle (*Stephanoaetus coronatus*) population in Durban, South Africa (McPherson et al. 2016a) that is at higher breeding densities than those reported in natural (non-urban) habitats. Both raptor populations nest in exotic pine (*Pinus* spp.) and eucalyptus trees (*Eucalyptus* spp., Malan and Robinson 2001; Tarboton 2001; Malan and Shultz 2002) that are currently the subjects of invasive plant removal. Invasive eucalyptus species are targeted (i.e., killed by ring-barking) by a government-funded nationwide management scheme called 'Working for Water' that aims primarily to provide poverty relief by employing task forces to control invasive vegetation and restore indigenous hydrological systems (Forsyth et al. 2004; Turpie et al. 2008). These dead trees stand defoliated and decaying for many years, resulting in a less sheltered nest site that will ultimately disappear. Therefore, conservation goals are in conflict (Dickie et al. 2014), which might affect other species such as African Fish-Eagles (*Haliaeetus vocifer*) in the Western Cape of South Africa, where eucalyptus trees provide the only suitable nesting source (Welz and Jenkins 2005). Such invasive plant removal is an area of conflict in many urban systems, particularly where they provide habitat or food for wildlife and where they affect animal taxa of high charismatic value such as birds and butterflies (Dickie et al. 2014). Further examples include the removal of invasive tamarisk (*Tamarix* spp.) in the USA that conflicts with conservation efforts targeting Willow

Flycatchers (*Empidonax traillii*), an endangered species that uses invasive trees for nesting (Shafroth et al. 2008; Schlaepfer et al. 2011), and the removal of Monterey Pine (*Pinus radiata*) plantations near Perth, Australia, that might result in declines in Short-billed Black Cockatoos (*Calyptorhynchus latirostris*) (Finn et al. 2009).

Direct conflicts can emerge between birds and humans, with one of the best-known examples being Australian Brushturkeys (*Alectura lathamii*) that construct massive incubation mounds from up to 4 tonnes of leaf litter, causing a clear conflict with garden owners, although many people welcome the species (Jones and Everding 1991). Australian Magpies (*Gymnorhina tibicen*) are an urban nesting species that exhibits extraordinary levels of aggression as they defend nest sites, attacking human intruders and causing injuries (Jones 2008). Another example is provided by parakeets (*Psittacula* spp.) nesting in towns and cities of Europe (Strubbe and Matthysen 2009). Rose-ringed Parakeets (*Psittacula krameri*) are secondary cavity-nesters and compete with native species (Strubbe and Matthysen 2007, 2009). The bulky communal nests of Monk Parakeets (*Myiopsitta monachus*) are known to cause damage to human infrastructure (Avery and Shiels 2017). Public stakeholders in an urban landscape have a strong influence on the management of dangerous large animals such as carnivores (Treves et al. 2006; Gehrt et al. 2010; Poessel et al. 2012). Likewise, one such avian example is provided by Crowned Eagles in the urban landscapes of southern KwaZulu-Natal, South Africa (McPherson et al. 2016a). They have occasionally been reported to prey upon livestock and pets (Boshoff 1990; Boshoff et al. 1994; McPherson et al. 2016b), with 24 verified attacks on Domestic Dogs (*Canis lupus familiaris*) documented between 2012 and 2017 in Durban and Pietermaritzburg (SC McPherson, pers comm). Crowned Eagles build huge nests that occasionally collapse, and artificial nest platforms have been used to replace such collapsed nest structures (Hoffman and Hoffman 2009). The placement of such artificial platforms becomes critically important in reducing conflicts between urban birds and their attacks directed at companion animals of urban residents.

While humans act as filters for avifauna within our cities through provisioning of food or nest sites, the ethics of such human behaviour have not been questioned in depth. Of course, interventions such as the provision of artificial nest sites (e.g., nestboxes, platforms) are important for the conservation of urban birds because even if they do not necessarily increase population density of a species, they promote our more intimate experiences of breeding birds (Fuller et al. 2012; Lepczyk et al. 2012). Public engagement increases awareness that is known to be a powerful tool in nature conservation (Devictor et al. 2010).

Future research addressing the nesting biology of urban species

There are many areas of research of urban nesting biology that deserve further attention, as we outline below. However, discussions about urban breeding birds are often dominated by the concept of the ecological trap. Therefore, we start this section by making some pertinent comments about future research concentrating on this concept. Maladaptive habitat occupation decision-making implies a preference for low-quality habitats over high-quality options, which can occur in heavily transformed habitats such as urban environments (e.g., Demeyrier et al. 2016). Such maladaptive behaviour causes species to fall into so-called ecological traps (reviewed in Kokko and Sutherland 2001; Schlaepfer et al. 2002; Kristan 2003; Battin 2004; Robertson and Hutto 2006). It is important to distinguish between an ecological trap and a habitat sink (see Kristan 2003). An ecological trap may have no population-level consequences (Robertson and Hutto 2006), but if organisms therein encounter adverse effects that result in the resident population not being self-sustaining, the area is instead described as a ‘habitat sink’ (Donovan and Thompson 2001). We use the term ‘ecological trap’ throughout this paper in accordance with the above distinction: a maladaptive behaviour displayed by a bird that does not necessarily result in population-level negative effects such as productivity being insufficient to offset mortality.

In regard to nest sites, there are four research areas that deserve attention. First, whilst there is good evidence that many bird species use native and non-native trees and shrubs, as well as a variety of anthropogenic structures as nest sites, we do not actually know whether such nest sites or nesting materials are in limited supply for birds in urban areas. Determining whether nest sites or nesting materials are limiting, especially for those species that predominantly avoid urban areas but that we may wish to target for conservation in urban areas, is important because, if limiting, future research might examine ways to improve urban nesting conditions in urban environments for such species, thereby promoting urban biodiversity conservation. Competition for nest sites and the effectiveness of measures to restore breeding habitat should thus be experimentally assessed before setting up any management measures for every target species. Currently, we are unsure whether the provisioning of artificial nest sites such as nestboxes or nest platforms reflects availability of natural nest substrates in the same urban habitats. Whereas the latter are permanent (as long as they remain accessible to birds) features of the urban landscape, artificial nest sites have to be maintained, the timing of which needs to be carefully orchestrated to minimise disturbance to urban birds. Therefore, studies that

examine the population status of urban bird communities before and after nest sites have been either experimentally or inadvertently provided or removed would enable us to examine whether availability of nest sites is limiting. This should be extended to broaden geographical coverage in answering such a fundamental question about nest site availability, because the abundance of cavity-nesting bird species increased in North America (Chace and Walsh 2006) but decreased in Australia (Luck and Smallbone 2010) with increasing levels of urbanisation. Patterns of nest site limitation may well vary between species with, for example, the provision of nestboxes with small entrance holes overwhelmingly promoting occupation by parids but deterring heavier and bigger species such as Western Jackdaws (*Corvus monedula*) from nesting.

Secondly, urban areas are considered to contain fragmented habitats because suitable nesting areas are usually separated by intensive land use such as transport infrastructure or buildings (Marzluff and Ewing 2001). Although isolation of such nesting habitat appears not to exclude most volant species in principle, in practice behavioural inhibition may preclude some species from nesting in such areas (Møller 2010), and certainly this should be investigated further. Moreover, habitat fragmentation may reduce the breeding success of at least some species. Marzluff and Ewing (2001) found that nest predators such as mammals, corvids and raptors thrive in urban areas where nests of native bird species are exposed to increased predation risk by virtue of being nearer to fragmented habitat edges where such predators patrol. Habitat fragmentation may also increase the time and energy needed to search for suitable nesting materials, and so further studies could usefully examine the nest-building behaviours of birds in urban versus non-urban areas.

Thirdly, the overwhelming majority of research examining the use of nest sites in urban areas has focused on birds in large cities (and conurbations), with far less research performed in smaller towns and cities. Therefore, future research could usefully examine the availability and use of nest sites in smaller urban centres, where temporal and energetic investment in searching for natural foods or nesting materials could be significantly reduced compared with birds breeding within dense urban matrices. Such research will help to increase our understanding of the importance of the configuration and size of habitat types to urban-adapted bird species.

Fourth, nestboxes and other artificial nest sites are widely provided for urban birds in North America and Europe, but we know very little about their value to birds. There is good evidence that building cavities and nestboxes act as ecological traps for birds in urban areas (Sumasgutner et al. 2014a; Demeyrier et al. 2016), but future research should test the generality of this effect. Furthermore, nestbox provision by humans varies considerably by geographic region, and future

research could examine the utilitarian value of provision of artificial nest sites in light of prevailing nesting conditions. For example, birds in non-temperate areas such as arid areas may use bushes or ground holes more commonly than in temperate regions. Furthermore, in tropical areas, the diversity of nest sites could be so high that green spaces such as parks within cities should be managed differently from those in temperate zones so that, for example, many more shrubs should be planted and maintained in those green spaces. Ultimately, future research in these areas will provide valuable insights into the influence of the native habitat on urban bird assemblages.

With regard to nest design, future studies should prioritise the following areas. From a methodological point of view, there are five important aspects that should be highlighted. First, it will be important to define more precisely what we mean by ‘anthropogenic nesting materials’. While it is common to include man-made materials only (e.g., plastics, fishing line, cloth) in this category of nesting materials (e.g., Wang et al. 2009; Sohi and Kler 2017; Biddle et al. 2018), it has been suggested that we might include other material associated with human activities such as hair from livestock and companion animals that we associate with, or materials from ornamental plants that we introduce into our urban gardens (Hanmer et al. 2017). Secondly, urban nest studies seldom employ state-of-the-art technology that is commonplace in other strands of field ornithology. We argue that the use of miniaturised, high-resolution wireless cameras to film nest-building behaviour (Ribic et al. 2012), biotelemetry to follow adult activities during the nest-building stage, and self-contained thermal monitoring units (Smith et al. 2015) to study incubation patterns at the nest will allow testing of some of the hypotheses addressing urban nest design. Thirdly, we need information from more species, particularly those exhibiting different nesting traits (e.g., use of ornamental layers), and from different regions of the world (e.g., South America, Australia/Oceania or Africa) where basic information about nest design is rudimentary at best (Table 2). Biddle et al. (2018) found evidence for interspecific variation in the use of anthropogenic material in different parts of nests, highlighting the importance of comparison when studying the effects of urbanisation on nest design (e.g., nest composition). Fourth, we need to perform more experimental studies, particularly to investigate the thermal ecology and humidity of birds’ nests and how they relate to breeding performance. Standardised methods should be used in all such future studies, as recently advocated for the incorporation of anthropogenic materials into birds’ nests by Provencher et al. (2017). While basic information about nest design in urban areas (especially regarding nest structures, ornaments and attachments) is desirable, if we want to understand how nest design varies with the urban landscape, we require landscape features (e.g., substrate, nesting

material availability) to be manipulated directly by researchers. Finally, following on from the successes of citizen science nest projects run by agencies in the UK [i.e., the British Trust for Ornithology's Nest Record Scheme (NRS)] and the USA (Cornell Lab of Ornithology's NestWatch project), we believe that there remains great potential for citizen scientists to contribute to our knowledge of nest design of urban birds (Greenwood 2007; Cooper 2017). We challenge other countries to engage with their citizen scientists to this end.

From a conceptual point of view, there are also several important ideas to consider in future studies. First, we need to investigate further whether the urban-associated changes in nest design translate into fitness consequences for the avian builders, focusing on both benefits and costs to them. This is crucial to understanding whether such changes are adaptive, facilitating urban colonisation. For example (experimental) studies that investigate whether there is a relationship between the use of anthropogenic nesting materials and fitness components such as breeding success or longevity would be very useful. A long-term perspective would be particularly important in such research, because some fitness costs might not be detectable from short-term studies (Suárez-Rodríguez and Macías García 2014).

Secondly, even though it remains to be tested, it is possible that different parts/layers of nests are influenced by different selective pressures in the urban environment, their fitness consequences for nesting birds could be different, and they might not be evenly responsive across urban gradients. Unfortunately, our current knowledge of nest components other than the lining layer is very scarce. However, there is evidence to suggest that urbanisation affects more than just the nest lining. For instance, urban-associated changes in nest location for several species (see above) suggest that components responsible for attachment of the nest to its substrate may be labile in urban birds. The outer (decorative) layer could also be affected by urbanisation due to the availability of certain materials in cities or changes in selective forces (e.g., nest predation, sexual selection). An interesting, yet unexplored, idea within this context is the potential role that structural changes in urban nests might have in attenuating some common problems in cities such as noise or light pollution.

Thirdly, common urban anthropogenic materials such as plastic and string can be harder to break or isolate as nesting material compared with natural materials (e.g., grass, moss), but we know very little about their manipulation by, and their costs (e.g., increased nest detectability by parasites or predators) to, avian builders. Similarly, our understanding of the selection of anthropogenic nesting materials is scarce. For example, we know little about whether birds select them based on size, weight or other characteristics, and the sensory modalities they employ to do so.

Fourth, our understanding from a mechanistic standpoint lags behind other strands of knowledge. For example, even in the case of regulation of ectoparasites in urban bird nests, we do not understand the mechanism of action of nest composition changes that could be explained by multiple non-mutually exclusive hypotheses (Suárez-Rodríguez et al. 2013; Hanmer et al. 2017). This mechanistic link is even less detailed regarding other functions, and should be a major objective of future studies. Furthermore, as in the case of the Mexican House Finches that use cigarette butts (Suárez-Rodríguez et al. 2013), a mechanistic point of view will also help to uncover potential physiological costs of changes in nesting biology followed by urban birds.

Finally, beyond our focus on arthropods, we should investigate the relationship of urban birds with other nest-dwelling biota such as bacteria or fungi. Relationships between microorganisms and many higher vertebrates including birds (McFall-Ngai et al. 2013; Colston and Jackson 2016) are profound, and are particularly important in the nest environment, where they can influence avian fitness (Cook et al. 2005; Grond et al. 2018; Peralta-Sánchez et al. 2018). Some studies have examined nesting materials and avian microbiota (e.g., Mainwaring et al. 2014b; Ruiz-Castellano et al. 2016) and suggested that this microbiological perspective could help us to unveil new effects of urban-associated changes in nest design.

Overall, the research gaps outlined regarding urban nest sites and urban nest design have important implications for conservation. First, the use of nestboxes has much potential as a conservation tool, but only if we possess knowledge of the fitness consequences of breeding inside nestboxes as opposed to alternative nest sites. This information is crucial for designing successful conservation plans for target species. The case of Common Kestrels (*Falco tinnunculus*) provides a good example of problems that arise from a lack of appropriate knowledge. This species is considered locally threatened (Jokimäki et al. 2018), but in inner-city areas the provision of nestboxes seems to act as an ecological trap for birds (Kettel et al. 2018), as they provide nest sites (Sumasgutner et al. 2014a) that attract birds into areas not offering sufficient diurnal rodents as prey (Sumasgutner et al. 2014b).

Secondly, little is known about the availability of different nesting materials in the urban environment and the fitness consequences of using anthropogenic versus natural nesting materials (see above). However, the association between plants in cities and nest composition (Lambrechts et al. 2017), as well as a recent experiment showing that providing natural nesting materials could reduce the amount of debris incorporated into nests (Lee et al. 2015), reveals a new way of promoting urban bird conservation. This will include promoting ornamental plants that provide natural nesting materials, or the direct provisioning of natural

nesting materials, if their shortage in cities represents a constraint for breeding birds.

Thirdly, bird nests might be useful indicators of environmental pollution (Furness and Greenwood 1993). For example, a positive relationship has been observed between the amount of debris in the area surrounding White Stork (*Ciconia ciconia*) nests, and that constituting the structure of the nests themselves (Jagiello et al. 2018). However, such an index of environmental pollution would need to be restricted to those bioindicator species that use nesting material in proportion to its availability in the environment, as opposed to birds that were actively selecting specific materials.

Urban avian conservation is an interdisciplinary field that requires several stakeholders to work together (Norris and Pain 2002; Greenwood 2007). This will not be an easy task, but the close association between humans and birds in these anthropogenic habitats provides exciting opportunities for research and conservation. We hope that this review shows that studying this overlooked aspect of avian biology can be very fruitful for expanding both our basic and applied ornithological knowledge.

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