



Review



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Movement ecology of urban birds: a review of tracking studies

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The world is urbanizing rapidly, impacting the movements of wildlife living within ever fragmenting urban habitats. Movement tracking by biologists can reveal the nature of these impacts for birds—particularly those that are prevalent within urban environments. We assembled and reviewed 123 studies examining the movements of birds in urban environments using movement tracking. We assumed that avian movements are driven by different internal states, such as foraging or reproduction, and synthesized the literature accordingly. We found that the number of studies per year increased over time, which was accompanied by a significant decrease in the average body mass of studied species over time. However, this was largely driven by studies employing non-satellite biologists, as opposed to generally more high-resolution satellite biologists such as GPS (interaction $t_{130} = 3.50$, $p < 0.001$). Furthermore, a tendency towards the study of structurally larger dietary-generalist species (e.g. Laridae spp.; 31.6% study effort) leaves significant gaps in our movement knowledge of smaller dietary-specialist species. Priority areas for future investigations are thus outlined, including focusing on smaller common urban taxa, such as songbirds generally, which form a significant but understudied proportion of our urban birds.

1. Introduction

Urbanization is intensifying globally, with 68% of people projected to live in urban areas by 2050 [1]. Understanding the impacts of rapid urban growth on biodiversity is of paramount importance to achieving the United Nations' Sustainable Development Goals, including sustainable growth of human settlements and protecting terrestrial ecosystems [2]. In the UK alone, 7% of land cover is already estimated to be urban, having increased by 30% from 1990 to 2019 [3]—a significant and worsening loss of natural habitat for biodiversity. Indeed, more than a third of Key Biodiversity Areas—sites defined by the International Union for Conservation of Nature as contributing significantly to the global persistence of biodiversity—currently contain infrastructure related to urban areas [4]. Despite this, many animals have adapted to live alongside us, or despite us, in the Anthropocene. This is especially true for species, or subpopulations of species, which have specialized in exploiting urban areas [5].

Birds are particularly widespread in the world's urban environments and can be particularly adept at exploiting them [6,7]. Indeed, more than 20% of the world's extant bird species are already found in cities [8]. Birds provide key ecosystem services [9] and can be important bioindicators of ecosystem functioning [10,11], for example, in monitoring the spread of human contaminants such as polybrominated diphenyl ethers [12]. However, anthropogenic activities associated with urbanization exert environmental stress and selection pressures on birds inhabiting urban areas, increasing oxidative stress and inflammatory responses, and ultimately, impacting survival [13]. Urbanization is thus a key driver of avian density and species richness [8,14,15].

The ability of birds to move successfully through the urban environment, satisfying needs, such as foraging (e.g. [16,17]), avoiding predators [18,19] or dispersing from natal sites (e.g. [20,21]), is crucial for their survival and fitness. Within a movement ecology framework [22] (figure 1), we might describe the urban environment according to external factors that impact movements of birds driven by their internal states (i.e. *why* move). This may be through direct impediment or enhancement of *how* to move (e.g. trees and buildings as corridors and barriers, respectively [23,24]), or indirectly by affecting intrinsic drivers of movement (e.g. artificial light at night (ALAN) inducing breeding states [25]) or navigation capacity (i.e. *where* to move, e.g. ALAN attracting autumn migrants [26,27]). The *how*, *where* and *why* ultimately determine the movement path of individuals, and thus the distribution of avian populations in space and time.

Many external factors associated with urbanization may impact the movement ecology of birds. ALAN is one such factor [28], attracting or repelling seasonal migrants [26,27,29], and potentially altering predation pressures and foraging site selection (e.g. [30–33]). Other examples include noise pollution by busy roads [34], or predation pressure from introductions of domestic cats (*Felis catus*) and dogs (*Canis lupus familiaris* [35–37]), which may induce avoidance of urbanized areas. Such avoidance shapes spatial behaviour and movement patterns of birds, and, indeed, it has been shown experimentally, in studies of flight initiation distance, that they reduce their escape distance in urban environments (e.g. [38,39]).

Understanding how external factors associated with urban areas influence avian movement ecology requires quantification of bird movement paths. To do this, arguably the most effective means is 'biologging', which can be defined as the use of animal-borne devices for gathering and/or transmitting data pertaining to an animal's movements, behaviour, environment and/or physiology [40]. Biologging devices take various forms depending on the study taxon, environment and research question being investigated [41]. These range from simple biologgers providing ad hoc data as to where an animal is in time and space, including passive integrated transponder (PIT) and very high frequency (VHF) radio biologgers, to satellite tags such as global positioning system (GPS) biologgers, which have enabled near continuous monitoring of animal movements [41,42]. The latter provides improved spatial accuracy compared with the satellite tracking alternative of Argos, a constellation of satellites that use the Doppler effect to determine the location of transmitters. However, although satellite tracking, in general, has enabled us to gather positional data at greater temporal resolutions than previously more prevalent non-satellite alternatives, they remain heavier and more expensive on average [41–44]. The method of data retrieval also presents logistical challenges to the researcher. For example, archival biologgers may confer advantages by storing data onboard the tag for later retrieval, reducing power requirements compared with those which transmit data to a receiver, and potentially reducing the mass of tags and/or increasing the quantity of positions recorded [43]. However, the retrieval of these tags to download data is not always possible, or is extraordinarily difficult [45],

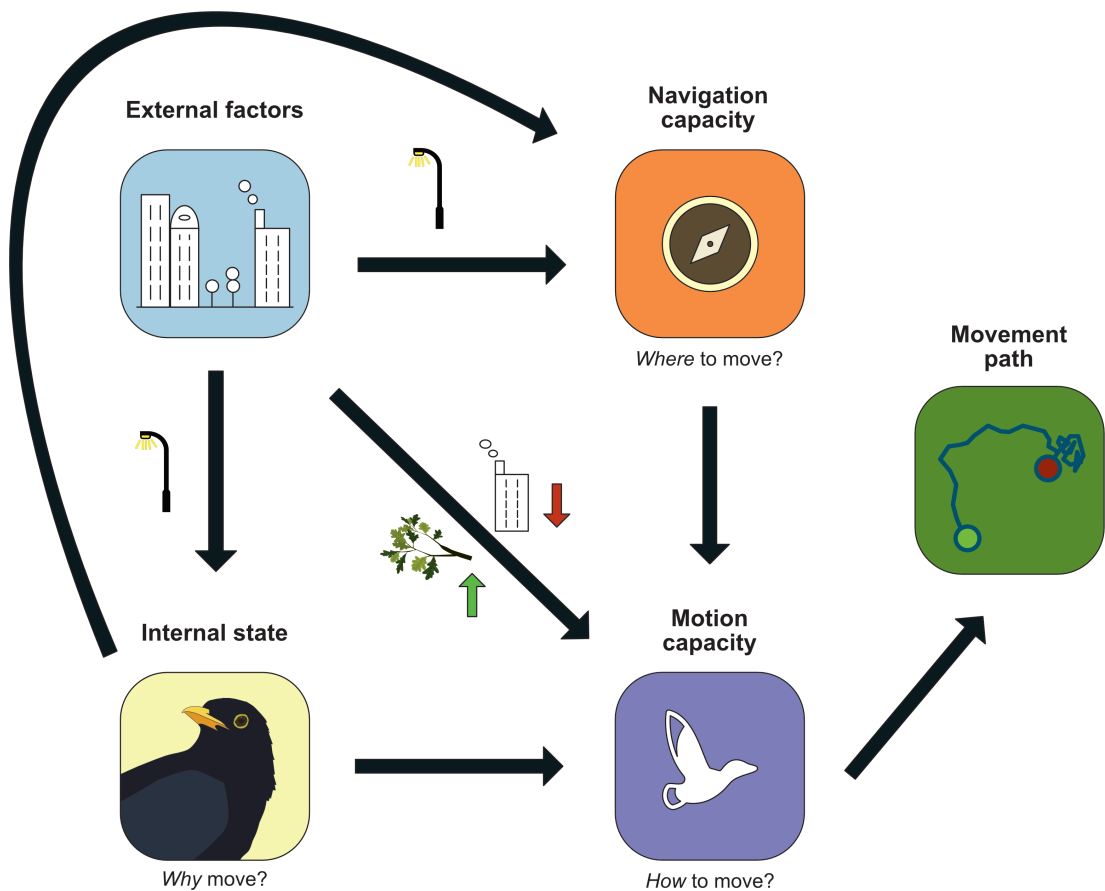


Figure 1. A movement ecology framework for studying avian movements in relation to external factors associated with urbanization (blue; city skyline). External factors, such as artificial light at night (ALAN; lit lamp post), may impact navigation capacity (*where to move*; orange; compass), for example, repelling seasonally migrating birds. This, in turn, affects motion capacity (*how to move*; purple; flying bird silhouette), or it may directly impede or enhance motion capacity through, for example, corridors and barriers such as treescapes or buildings. External factors, such as ALAN, may impact birds' internal states (*why move*; yellow; blackbird profile) by, for example, inducing breeding states which, in turn, drive movement determined by navigation and motion capacity. Ultimately, this determines the movement path (green; abstract movement path). Adapted from Nathan *et al.* [22].

especially for species that are difficult to capture in the first instance for tag deployment (e.g. *Corvus* spp. [46]). Such methodological decisions are particularly important when planning a biologging study in urban environments where, for example, tall buildings may interfere with data transmission or radio frequency detection, and the capture of animals for tag deployment/retrieval may be made difficult due to public interference or opposition [47,48].

Advances in biologging technology, including associated miniaturization and power efficiency optimizations, have naturally resulted in an increased number of research outputs using them across a growing diversity of animal taxa, including birds (e.g. [42,49,50]). Despite this and the acknowledged importance of understanding the impacts of urbanization on avian biodiversity [51], research employing biologgers to quantify avian movement in urban environments has received surprisingly little attention to date. For example, although such research may be particularly effective at answering questions regarding functional connectivity in urban areas, this was surprisingly lacking in a review of the topic by LaPoint *et al.* [52]. Therefore, we sought to address this by undertaking a literature review of studies using biologging to investigate bird movements in urban areas.

We endeavoured to address two specific objectives with this review. The first was to describe the discipline of urban bird tracking in terms of its current status, the range of studies that have contributed to our current understanding and directions for future research. In so doing, we tested temporal trends in the literature base, geographical and taxonomic distributions of studies, and trends in biologger types used. The second objective was to synthesize the outcomes of these studies, aggregated by pre-defined themes according to the types of movement examined in the study, and to a logical sequence of internal states driving avian movements (figure 1) [22]. From the synthesis of these studies,

we aimed to provide novel insights, interpretation and theoretical reflection on the use of biologgers to study urban bird movements.

We expected to find that urban bird biologgging research would: (i) have increased at a greater rate than that across all types of environment generally, given the stated timeliness of such research; (ii) be geographically biased towards wealthier regions, particularly across the Global Northwest in Europe and North America, given the relatively large financial investment required for such research and the acknowledged spatial biases in locations of such ecological research [53]; (iii) be concentrated on larger and thus arguably ‘easier to study’ urban bird species such as gulls (*Laridae* spp.) and pigeons (*Columbidae* spp.); and (iv) be increasingly concentrated over time on smaller species, in all forms of biollogger geopositioning (satellite and non-satellite), given advances in the miniaturization of tags and the expectation that research will attempt to bridge previous taxonomic gaps.

2. Material and methods

2.1. Core literature search

We conducted a literature search using PRISMA guidelines [54] (see flowchart in electronic supplementary material), assessing the use of tracking biologgers to quantify the movements of birds in urban areas. Our literature search consisted of two stages: first, a search by ‘topic’ of the Science Citation Index Expanded (SCI-Expanded) database of the Web of Science (accessed 19 November 2024); then a supplementary search via backward citation tracking—identifying potentially relevant papers by screening the reference lists of studies identified during the first stage. The database search was conducted without limit on document type, over an unlimited time span, and focused on four key terms: (i) ‘urban environments’; (ii) ‘birds’; (iii) ‘movement’; and (iv) ‘biologgers’. Accordingly, the following indicative list of keywords and Boolean operators was included in the search matrix (see full exhaustive list and search results in electronic supplementary material): ‘urban*’ OR ‘city’ OR ‘town*’ OR ‘anthrop* habitat*’ OR ... AND ‘*bird*’ OR ‘avian’ OR ... AND ‘move*’ OR ‘cross*’ OR ‘dispers*’ OR ‘fly’ OR ... AND ‘biologg*’ OR ‘logger*’ OR ‘GPS*’ OR ‘tag*’ OR ‘tracker*’ OR

The search returned 202 unique papers, which were initially screened for inclusion by reference to the abstract, keywords, title and methods. Through reading the literature cited section of each paper, eight further papers were identified that met the aims of this review, which were not initially identified by our search. Papers were then excluded according to the following criteria: (i) not concerning birds ($n = 23$); (ii) not concerning movement ($n = 6$); (iii) no movement tracking by biologgging ($n = 15$); (iv) no results presented or discussed pertaining to urban movement ($n = 41$); or (v) not a primary research article ($n = 2$). Papers excluded according to (iv) either presented no results pertaining to urban areas (as defined by the paper’s authors) or did not discuss movements within urban areas. Conversely, any paper in which birds’ movements were described in urban areas, however few, were included. However, studies not describing *how* bird movements were affected by urban areas were accordingly excluded under (iv). Based on these criteria, 87 papers were excluded, resulting in 123 primary research articles being retained. Since we aimed to capture as much of the relevant literature as possible, our search terms were very broad and thus also captured a large proportion of non-relevant papers (see full list of excluded papers in electronic supplementary material).

Because it was not feasible to distinguish with certainty between primary research investigations and secondary analyses, each retained paper was treated as a separate study (the terms ‘paper’ and ‘study’ are thus used interchangeably henceforth). Retained papers were analysed in detail and for each publication year, focal species (following the eBird taxonomy [55]), tracking method(s) and host countries of study were recorded. For each species, we obtained its average body mass using the AVONET database [56]. Relevant body masses in AVONET were originally sourced from Dunning [57] or Birds of the World [58] and are averaged across the sexes (i.e. there is a single value per species). While we recognize that this could be misleading where species are significantly sexually dimorphic (e.g. raptors), we did not distinguish between the sexes because we are only investigating general trends in biollogger use at a species level. Geographical aggregation of studies was conducted at the country level because of the relatively small number of studies in the literature pool that limits the conclusions that can be generated from finer scale aggregation. Modally, most papers constituted only a single study per city, for example. Furthermore, studies differed in the reported precision of location data from the number of fixes per location to more coarse coordinates of a large study, and everything in between.

2.2. Trends in the literature

To enable testing of the taxonomic distribution of study species, we assigned a measure of ‘taxonomic study effort’ across the literature by giving a value of ‘1’ to each focal species studied in each paper, including where multiple species were investigated. Accordingly, the taxonomic study effort totalled 136 for 123 papers identified. Likewise, we also assigned a measure of ‘geographical study effort’ by country, deriving a total of 143 for the pool of papers.

We synthesized bilogger types used in studies by ge positioning method, being ‘satellite’ or ‘non-satellite’. Where multiple types of loggers were used in a single study ($n = 12$), we took the ‘finest ge positioning method’ (henceforth: ‘ge positioning method’) as the type of bi logger employed, which theoretically should produce the finest resolution data overall. We rationalized that these would be the tags for ge positioning by satellite, because non-satellite loggers, such as PIT or radio, will largely not be able to capture as full an extent of a species’ movement range, nor as consistent positional data, such as loggers using GPS [41–43].

In addition to the original literature search described above, two separate nested literature searches were conducted to enable a comparison of the number of publications per year of avian movement logging studies in all environments compared with those that explicitly referenced urban environments. Likewise, these searches were performed by ‘topic’ via the ‘SCI-Expanded’ database of the Web of Science in the same manner as above, but with the keyword ‘tag*’ removed from the ‘loggers’ terms for both searches (since this was too broad for a wider search). For one search, the ‘urban environment’ terms were removed. To each pool of returned papers was added the same five papers identified as described above (after exclusion criteria), which were not otherwise returned by the search. This resulted in final counts of 3900 and 166, respectively. Not all papers were read for this comparison, as we were only interested in the publication trend (if research in urban areas has increased at a greater rate than the general trend).

2.3. Synthesis of key themes by movement type

We defined movement types according to internal states driving avian movements (figure 1) [22]. We defined six states in a logical temporal sequence, these being: (i) foraging (including general feeding during the non-breeding season as well as central place foraging during breeding attempts); (ii) roosting; (iii) disturbance avoidance (including predator avoidance, parasite avoidance and anthropogenic avoidance e.g. ALAN); (iv) reproduction-related (including territory prospecting, courtship, nest building and territorial defence); (v) post-juvenile dispersal; and (vi) post-breeding and annual migration. For each of the movement types within a paper, we assigned a value of ‘1’ when it was evaluated and ‘0’ when it was not. Where none of the defined movement types was evaluated, for example, when birds were tracked but the aim was to quantify urban pollution (e.g. [59]), that study’s aims were evaluated and recorded in more detail.

2.4. Statistical analyses

The distributions of both taxonomic and geographical study efforts were analysed using Pearson’s χ^2 -tests, both against a null uniform distribution. A further Bonferroni-corrected χ^2 -test was conducted to assess whether our expectations were met regarding the disproportionately greater number of studies in Europe and North America versus the rest of the world.

Temporal trends in the use of bi logger types described above, on species of varying body masses, were assessed by fitting a generalized linear model (GLM, gamma) with log link, with species’ average body mass as the response variable, and publication year (continuous) and bi logger ge positioning type as explanatory variables. Two publications from 1990, 14 years before the next earliest publication [60,61], were excluded from this analysis as they skewed the data greatly. The difference in the overall mean of logged average species’ mass between bi logger types was assessed with a Welch two-sample t -test.

The difference between the trends in the number of publications per year, in each search category (all environments versus urban only) of the latter two searches, was assessed by fitting a GLM (Poisson) with log link, using publication count as the response variable. Publication year, search category and their interaction were included as fixed effects. Publication year terminated at the end of 2023 for this analysis of temporal trends in the number of logging publications only, as 2024 was not complete at the time of our literature search.

Data were all analysed using R v. 4.3.0 [62]. Appropriateness of tests, including associated families and link functions, was determined by the nature of the data, visual inspection of histograms and associated residual plots and analysis of deviance. Taxonomic silhouettes in figures were created using the 'rphylopic' package [63] pulling from PhyloPic [64].

3. Results

3.1. Temporal trends in the number of biologging publications

Contrary to our expectation that the rate of increase in publications of urban avian biologging studies would be greater than the general rate, we found no such effect (GLM, interaction effect of publication year and search category ('urban only' as opposed to 'all') in full model: $z_{62} = 1.53$, $p = 0.13$; table 1). Indeed, although publications of avian movement biologging studies in urban environments began much later than in other environments (e.g. hilly plateaus in Missouri, USA [65]) in 1990, the increase in the number of publications has followed a largely similar curvilinear increase to 2023, peaking at 23 in 2021.

3.2. Locations of biologging studies

In total, the 123 studies took place in 25 different countries, with 64.3% of them taking place in just four: USA ($n = 46$), Canada ($n = 20$), Australia ($n = 14$) and Spain ($n = 12$; figure 2). Accordingly, the geographical distribution of studies deviated significantly from a uniform distribution ($\chi^2_{24} = 388.60$, $p < 0.001$). North America was represented in 46.2% of all studies, closely followed by Europe (34.9%) and Oceania (10.5%). Less than 10% of studies took place in the rest of the world, including Africa, Asia and Central and South America. In accordance with our expectations, the number of studies in Europe and North America combined was significantly greater than the number across the rest of the world combined ($\chi^2_1 = 55.39$, $p < 0.001$).

3.3. Avian species coverage and body masses in biologging studies

In the 123 publications, movements of 83 different bird species were reported, belonging to 14 different orders (figure 3). Taxonomic biases were apparent, with gulls investigated in 43 publications, representing 31.6% of the study effort. Accordingly, the distribution of study effort across orders deviated significantly from a uniform distribution ($\chi^2_{13} = 207.20$, $p < 0.001$). The median of the average mass of species studied was large at 668.2 g (between kererū, *Hemiphaga novaeseelandiae* (a pigeon native to New Zealand), and California gull, *Larus californicus*), far larger than the median of the average mass of all species in the AVONET database at 35.5 g (using the eBird taxonomy [56]).

3.4. Tracking methods employed in biologging studies

The principal geopositioning method across studies was by satellite ($n = 90$ species), the remaining being non-satellite ($n = 46$; including radio tracking, PIT tag, Bluetooth low-energy, etc.). Between 1990 and 2016 (inclusive), 36.1% of studies used satellite geopositioning methods, increasing to 65.8% between 2017 and 2020 (inclusive) and 96.9% between 2021 and 2022 (inclusive). The percentage of studies employing satellite geopositioning methods declined to 69.0% between 2023 and 2024 (inclusive).

Overall, the average mass of species studied decreased significantly across publication years (excluding 1990; see §2; GLM, effect of publication year in full model: $t_{132} = -4.05$, $p < 0.001$; table 2; figure 4). Although body mass was predicted to be lower at the intercept in species tracked by satellite methods (GLM, effect of geopositioning method in full model, for satellite as opposed to non-satellite: $t_{131} = -3.478$, $p < 0.001$), there was a significant interaction between publication year and geopositioning type, such that the change in body mass of species tracked by non-satellite methods (generally decreasing) differed significantly from that for studies employing satellite methods (generally increasing; GLM: $t_{130} = 3.50$, $p < 0.001$). Indeed, the mass of species tracked by satellite methods ($\bar{x} = 1067.20$, $\sigma = 779.2$) was significantly higher over the publication period (including 1990) than that tracked by non-satellite methods ($\bar{x} = 363.90$, $\sigma = 825.1$; $t_{54} = -8.91$, $p < 0.001$).

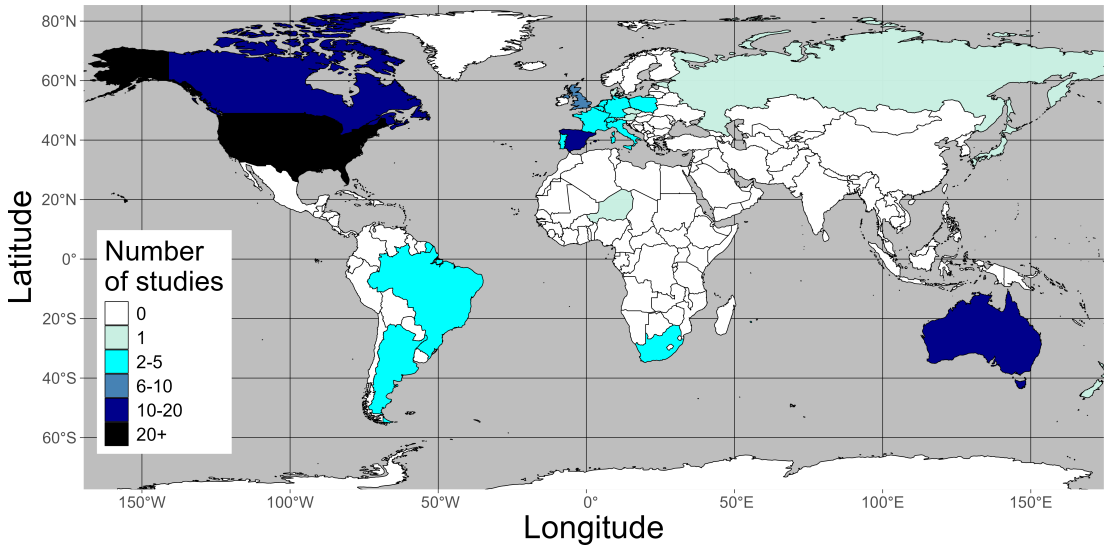


Figure 2. Global map of study effort by country, showing the number of urban biologging studies of bird movements (see S2 for details of the literature search conducted).

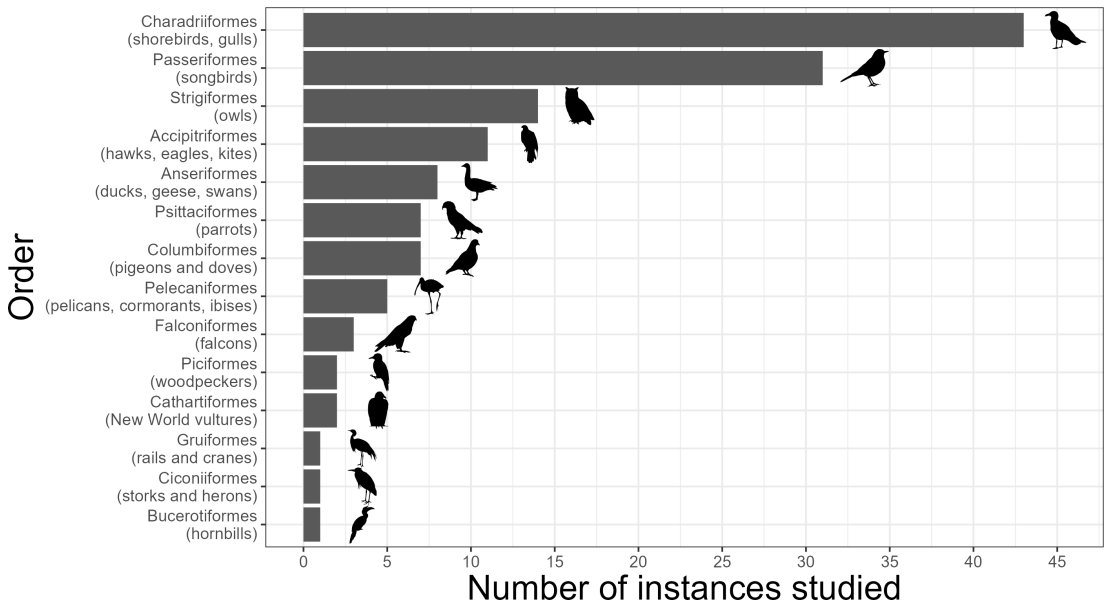


Figure 3. Taxonomic study effort in studies of movements of urban birds by order of focal species, arranged descending by number of instances studied (see S2 for details of the literature search conducted). Note that some avian orders, such as songbirds, are markedly more speciose than others. Passeriformes account for approximately two-thirds of all bird species [66]. Furthermore, many avian orders found in urban areas are not listed here, as there were no studies tracking their movements per our review. This should be particularly considered when identifying species or clades as subjects for future research.

Table 1. Results of the Poisson GLM investigating publication rate of urban bird tracking literature, with number of publications as the response variable, for the 'urban only' literature search as opposed to 'all environments'. Estimates are reported on the log scale.

fixed effects	estimate	s.e.	d.f.	z	p(> z)
intercept	-216.90	4.10	65	-52.86	<0.001
publication year	0.11	0.00	64	54.09	<0.001
search category (urban only)	-5.18	31.92	63	-1.62	0.105
publication year * search category (urban only)	0.02	0.02	62	1.53	0.127

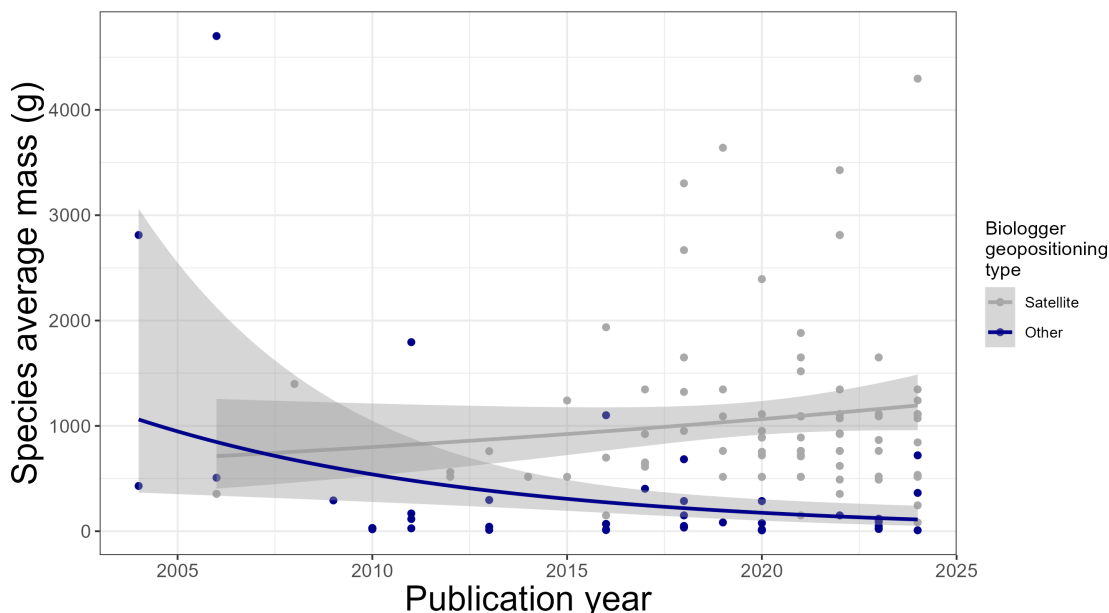


Figure 4. Temporal pattern in the body masses of focal species reported in biologging studies of movements of urban birds (see S2 for details of the literature search conducted) using satellite (grey) or non-satellite (blue) tracking methods. GLM fit is overlaid for each tracking method with 95% confidence ribbons.

Table 2. Results of the gamma GLM investigating the mass of species tracked by different biologger ge positioning types over time, with average mass of species tracked as the response variable, for satellite ge positioning methods as opposed to non-satellite. Estimates are reported on the log scale.

fixed effects	estimate	s.e.	d.f.	t	p(> t)
intercept	232.60	56.03	133	4.15	<0.001
publication year	-0.11	0.03	132	-4.05	<0.001
ge positioning type (satellite)	-283.50	81.52	131	-3.48	<0.001
publication year * ge positioning type (satellite)	0.14	0.04	130	3.50	<0.001

3.5. Movement types in biologging studies

Movements driven by foraging were most often evaluated in studies, with more than half (i.e. $n = 71$) investigating instances of foraging movements (figure 5). Causes of bird movement were evaluated and then grouped into disturbance avoidance ($n = 17$), roosting ($n = 13$), reproduction-related ($n = 10$), post-juvenile dispersal ($n = 8$) and lastly post-breeding and annual migration-type movements ($n = 3$). In 30 of the 123 reviewed papers, the internal state of birds motivating their movements could not be identified because the main aim of such studies was not to quantify the type of avian movements.

4. Discussion

Although we have been able to track animal movements at relatively high temporal and spatial resolutions for more than six decades using biologgers (e.g. [67,68]), it is clear that such tracking of urban birds is still in its infancy. We reviewed the literature and found a clear positive temporal trend in the publication of studies investigating movements of urban birds using biologgers. Contrary to our expectations, the rate of increase was not significantly greater than that of biologging studies of avian movements generally, possibly reflecting a lack of focus on this critical area of research [5,52,69,70]. This increase in the number of urban studies was marked by an over-representation of avian taxa, such as gulls, especially across the Global Northwest in Europe and North America, consistent with our expectations (figures 2 and 3). In synthesizing these studies according to the movement types examined, we identified several key themes.

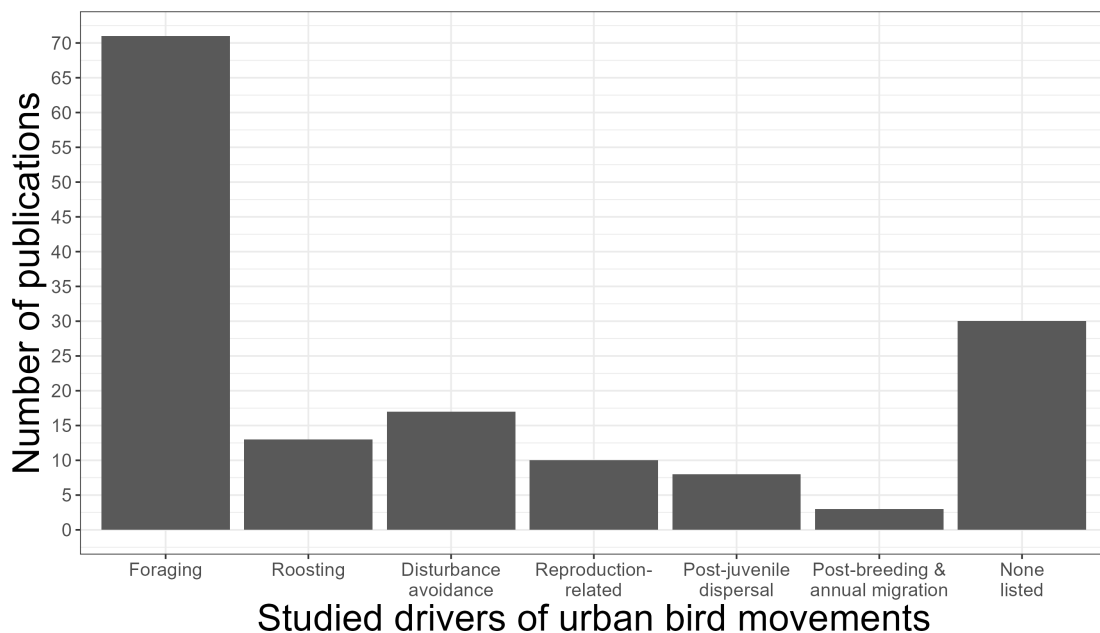


Figure 5. Number of publications returned by our literature search, categorized by types of movement evaluated (defined by internal states driving movement; see S2 for details of the literature search conducted).

4.1. Studied drivers of urban bird movements

4.1.1. Foraging

More than half of the biologging studies we identified investigated urban movements driven by foraging (figure 5). Irrespective of feeding substrate (e.g. ground, aerial), the daily activity budget of many bird species is spent foraging [71], and it is one of the most intensive central-place and longer distance movement types that birds undertake on a regular basis. Feeding movements might be considered one of the simplest movement behaviours to distinguish using velocity and/or tortuosity estimates derived from recorded movement paths (e.g. [72,73]), or modern tri-axial accelerometry measures (e.g. [74–76]). As such, it is perhaps unsurprising that most studies have investigated the foraging movements of urban birds.

We found that across studies of larger birds with generalist feeding strategies (e.g. gulls, pigeons), which might be considered highly ‘tolerant’ of urban environments [70,77], foraging movements were often towards or within urbanized areas (e.g. [78,79]). Some of these birds are able to take full advantage of temporally and geographically predictable anthropogenic resources available in urbanized environments, such as at landfills or fisheries (e.g. [80–82]), which can offset low food availability, especially during inclement times of year (e.g. [83–85]).

Studies that examined the movements of larger birds with more specialized feeding strategies, such as raptors, largely found that they were less likely to use urban areas to forage than larger birds with more generalist feeding strategies. Largely, nocturnal owl species (*Strigidae* spp.), for example, were found mostly to cross urban land cover quickly to access preferred foraging grounds (e.g. [86,87]), while bald eagles (*Haliaeetus leucocephalus*) that appeared to specialize on foraging landfill refuse in Vancouver, BC, Canada, were largely only a sub-population of subadults, most others visiting the landfill only occasionally and to rest rather than forage [88]. However, the latter provides an interesting case study demonstrating how urban areas may provide an important resource to first-year raptors, which typically have a lower survival rate than adults [89], helping to increase their population size.

Studies investigating the foraging movements of smaller passerine species in urban areas were few in number. However, Cox *et al.* [90] reported negative impacts of urbanization on the garden feeder visits of blue (*Cyanistes caeruleus*) and great tits (*Parus major*), inferring that this was related to road density. Furthermore, Vangestel *et al.* [91] reported smaller home range sizes in urban house sparrows (*Passer domesticus*) in areas of greater urbanization. They inferred from the narrower width of feather growth bars in the urban birds, often used as a proxy for nutritional availability during the growth of the feather, that these birds experienced nutritional stress as a result of the greater levels of habitat patch disconnectivity than experienced by those birds living in rural areas.

Overall, the impacts of urbanization on foraging movements of birds were often closely related to life-history traits such as dietary generalism and body size of species. These avian traits are often linked to urban tolerance, with, for example, Callaghan *et al.* [92] finding that larger Australian species with broader foraging niches (e.g. Australian white ibis, *Threskiornis molucca*) were more tolerant of urban environments. Neate-Clegg *et al.* [77] also found that there was a positive relationship between the width of the foraging niche and the degree of urban tolerance in birds generally, and more urban-tolerant birds also tended to possess greater dispersal ability as measured by the Hand-Wing Index [93]. We found some concurring evidence in our literature search that species, such as gulls and pigeons, with more generalist diets, moved towards and exploited anthropogenic foraging resources more than dietary specialists. Although the former were often larger birds with generalist diets, too little evidence exists for smaller birds to make any generalizations regarding body size and its direct impact on foraging movements, highlighting the need for broader taxonomic representation in future urban studies of avian foraging movements. These studies also highlight an understudied aspect of urban foraging by prey species—such as pigeons exploiting anthropogenic food sources—in that by aggregating in large numbers, they can act as a secondary attractant for predators such as peregrine falcons (*Falco peregrinus*). These prey hotspots may fundamentally alter the foraging movements of urban predators by concentrating hunting effort within the urban core, warranting further investigation.

4.1.2. Disturbance avoidance

A surprisingly small number of studies examined the movements of urban birds in relation to disturbance (figure 5). Urban intolerant species are, by definition, more likely to avoid urban areas and thus sources of anthropogenic disturbance [77]. This makes understanding the impact of urban disturbance on the capacity of such species to move all the more important to study but paradoxically, all the more difficult to observe or quantify, perhaps explaining the relative dearth of empirical studies.

Of movement studies examining urban disturbance, Ladin *et al.* [94] found that two phylogenetically closely related passerine species (according to DNA sequencing) were highly different in their avoidance of roads in the post-fledging phase despite originating from similar forest fragment nesting areas in both Delaware and Pennsylvania, USA. Specifically, they discovered that forest-specialist wood thrushes (*Hylocichla mustelina*) avoided roads more frequently than did habitat-generalist grey catbirds (*Dumetella carolinensis*). Further study of a highly urban-tolerant species evidenced that Canada geese (*Branta canadensis*) were highly resistant to deliberate forms of human disturbance, moving only short distances, if at all, when disturbed with laser devices in Ohio, USA [95]. In Copenhagen, Denmark, a much smaller species, short-toed treecreepers (*Certhia brachydactyla*), displayed high urban tolerance by apparently moving freely between habitat patches isolated by urbanization [96]. On the other hand, avoidance was apparent in the movements of juvenile burrowing owls (*Athene cunicularia*) occurring in urbanized areas of New Mexico, USA, in that they avoided urban land cover at night, despite it containing suitable habitat [97]. This contrasts with findings of Rodriguez *et al.* [33] in Argentina, suggesting that proximity to ALAN was a key variable explaining nest-site selection by burrowing owls, using space under streetlights preferentially to forage at night and, thus, actively selecting for more urbanized burrow sites.

Overall, the synthesis of the effects of urban disturbance on the movement ecology of birds from the literature is limited, despite this being one of the key drivers of avian urban movements, because the number of movement studies explicitly investigating urban disturbance is small and rather limited in coverage of taxonomy and potential sources of urban disturbance. Particularly surprising was a lack of research coverage in terms of the extent to which disturbance by urban roads impacts the movement capacity of smaller, common urban bird residents such as songbirds.

4.1.3. Other internal states

A limited number of studies have investigated the roosting movements of urban birds (figure 5). Urbanization can negatively impact the daily movement patterns of such birds by reducing the connectivity of key routes between roosting sites and those where they feed or gather in pre-roost assemblages (e.g. [98–100]).

Investigations of movement related to post-juvenile dispersal were also few in number (figure 5), but Ausprey & Rodewald [101] found that fledglings of urban-adapted northern cardinals (*Cardinalis cardinalis*) moved into more urban areas of Ohio, USA, while those of less urban-adapted Acadian

flycatchers (*Empidonax vireescens*) moved away into areas of higher Amur honeysuckle (*Lonicera maackii*) cover. This is consistent with generalist species being more well adapted to urban environments.

We also found a few studies that examined urban movements of birds during post-breeding and/or on annual migration (figure 5). However, as a rare exception, Dykstra *et al.* [102] investigated the post-breeding migration of mallards (*Anas platyrhynchos*) in Connecticut, USA. They found that movements of post-breeding parents from nest sites to brood-rearing sites were reliant on small connecting streams. They inferred that the fragmentation of these streams by urbanization in their study area may be responsible for the higher-than-average duckling mortality they documented, possibly resulting from an inability to access or locate optimal brood-rearing sites [102].

A small number of recent studies directly examined movements of urban birds related to reproduction, such as during courtship, territory prospecting, etc. (figure 5). Stewart *et al.* [103] found that grey hawks (*Buteo plagiatus*) in urban areas of Texas, USA, defended smaller territories than those breeding in more rural areas. Jarrett *et al.* [104] found that urban blue tits in Scotland travelled nearly a third further than their forest counterparts to provision broods, ultimately providing lower quality food, with caterpillars constituting a smaller percentage of urban broods' diets than those in the forest.

Many studies have not explicitly inferred any drivers of bird movements (figure 3). Some studies (e.g. [105,106]) only described habitat associations of focal species, while others (e.g. [59,107]) simply employed biologgers to investigate birds as vectors to examine movements of seeds, zoonotic disease or atmospheric pollutants.

4.1.4. Use of biologgers to study urban bird movements

With advances in technology, including the miniaturization of biologgers, we predicted that the tracking of smaller birds would increase in feasibility and thus would occur increasingly in the more recently published studies. We did find such a trend in deployment of non-satellite biologgers, but not in satellite analogues (figure 4). Despite miniaturization of both tag types, the increased battery capacity and antenna length requirements of satellite-linked tags still necessitate a higher weight threshold. Larger birds thus allow for a more ethically robust deployment by ensuring the tag remains a lower percentage of the bird's total mass [108], even as hardware becomes smaller. This, combined with the generally increasing economic and time cost of increasingly complex ecological research [109], probably contributes to the dearth of studies on smaller birds that we observed.

We found that the earliest studies tracking urban birds with satellite telemetry were Rose and colleagues [110,111]. Despite animal-borne GPS devices being used since the 1990s (e.g. [112,113]), the miniaturization of such satellite-based hardware has been slow to advance. Advances in GPS device software have also taken time, such that only recently have variable temporal schedules for data collection been made available by tag manufacturers to manage the battery life of tags and thereby maximize data acquisition volumes (e.g. [78,114]). The advantages of remote satellite telemetric technologies, such as reduced field effort and greater potential spatial and temporal resolutions, may still sometimes be outweighed by logistical challenges in their deployment in urban environments, such as limited access to suitable receiver positions due to tall buildings. Older radio telemetric technologies may even sometimes offer advantages over their satellite-based counterparts, such as the ability to triangulate their position more accurately after detachment, enabling more reliable recovery and reuse of devices. Perhaps most importantly, in a world of increasingly limited resources for field studies, satellite biologgers remain relatively high cost compared with other biologging options, especially in smaller sizes. It is thus perhaps not surprising that the use of satellite geopositioning devices to track urban bird movements has thus far been relatively limited, especially for smaller birds. However, if the research gaps we have identified are to be effectively addressed, we must find ways of reducing their shortcomings, in order that we might profit from the greater level of insight they can offer.

4.2. Future research directions

4.2.1. Addressing taxonomic and geographical gaps in knowledge of avian urban movements

We found that nearly two-thirds of the study effort in publications we reviewed took place in Australia, Canada, Spain and the USA, findings that were also reflected in a review by Iverson *et al.* [50] of migratory movements of small birds using GPS and platform transmitter terminal technologies (figure 2). The concentration of studies in Europe and North America was so great as to significantly

outnumber those in the rest of the world combined. This bias towards research concentrated in the Global Northwest is well established in ecological research [53], but we highlight the need for urban movement studies of birds in the Global South and East. Of particular concern is the lack of coverage of the world's tropical cities; this means that we lack information on the effects of urbanization on bird movements for many such species from highly biodiverse areas of the world. Indeed, such information is non-existent for some of the globe's Key Biodiversity Areas most affected by urban infrastructure, such as nearly all of Africa [4]. This is especially pertinent as the fastest urbanizing regions of the world are presently in Africa and the Global East [1].

Nearly 33% of taxonomic study effort was concentrated on gull species (i.e. Charadriiformes) in our review (figure 4), outweighing those conducted on the much more speciose Passeriformes, an order that accounts for nearly 66% of all bird species [66]. Although this is perhaps unsurprising given the prevalence of gulls in cities around the world [115], it is probably also a function of their ease of study, given their colonial nesting behaviours on urban buildings, large size that enables straightforward capture and ease of biologger deployment (e.g. [114,116–118]). In this respect, our expectations were met in regard to the taxonomic distribution of studies. It is noteworthy that many of the Canadian and Spanish studies (e.g. [119]) used data from pre-existing 'larger' datasets gathered from gull species, highlighting the wealth of information that can be obtained from shared data between studies.

Concentrating research on common species is likely valuable in understanding generally how urbanization impacts avifauna, because they are both potentially the most representative birds of the broader effects of urban factors impacting movement, and those whose losses will result in the most pronounced cascades of further species loss [120]. While the current literature is dominated by larger bodied dietary generalists, such as gulls and pigeons, a comprehensive understanding of urban avian ecology requires a broader taxonomic approach. To move beyond the limitations of current data, future research should prioritize smaller common species and those with more specialized foraging niches. For example, expanding biologging efforts to include widespread passerine groups such as thrushes (Turdidae spp.), sparrows (Passerellidae spp.), and finches (Fringillidae spp.)—particularly across the understudied tropical regions—will provide a more nuanced perspective on how diverse life-history traits influence bird movements in the urban matrix.

We argue that more research effort is also warranted when species have recently colonized cities from non-urban native areas (e.g. long-eared owls, *Asio otus* [121]; ring-necked parakeets, *Psittacula krameri* [122]) or where their natural historic range has been fragmented through urbanization such as in barred owls (*Strix varia*) in South Carolina, USA [123]. This would help to further our understanding of the mechanisms of urban invasions, whether human-introduced or otherwise.

In addressing these information gaps in future studies, it will be of great importance to ensure consistency when defining how 'urban' an area is, especially in regions such as the tropics, where human-modified landscapes often interweave heavily with green space. We noted that in some of the studies we reviewed, the distinction between urban and non-urban environments was not well defined. Often, urban areas were defined by subjective categorical landcover definitions (e.g. [124,125]). The complexity of some habitats for birds, such as mosaics of heavily modified space within otherwise more natural areas, cannot always be captured by broad-scale categorical definitions of large areas as urban or non-urban, especially when the response, such as movement behaviour, is highly nuanced. We advocate instead for the use of a globally relevant, repeatable, objective metric such as ALAN [126] or housing density (as in e.g. Dellinger *et al.* [127]) to quantify urban land cover. The quasi-continuous, rather than categorical, nature of such measures should confer significant advantages to data users during analysis. By standardizing such measures in future research, we can ensure greater comparability across studies, accelerating a scientific consensus on avian movement patterns in urban environments.

4.2.2. The future of tracking urban bird movements using biologging

We are excited by the potential of biologging research to quantify urban bird movements with new technologies, such as Bluetooth low-energy devices [128]—lightweight tags employing the Find My network via local mobile phones that are highly prevalent in urban areas—potentially opening up a great range of research opportunities not previously attainable. An example might be the tracking of a large number of species simultaneously across their entire range in high-density urban environments, potentially documenting species' interactions and/or social networks. Furthermore, the high density of human observers in cities offers a unique opportunity to integrate biologging data with citizen science platforms like eBird or iNaturalist. Such multi-source datasets could validate tracking-derived

movement models with large-scale presence-only data, providing a more robust picture of urban habitat use [129].

Despite the continuing development of new technologies, many existing technologies are presently underused. For example, Yoda *et al.* [85] was the only study of urban birds that we identified that deployed video loggers attached to birds as well as satellite biologgers, but not simultaneously. This technology enabled high-fidelity behavioural analysis to be conducted and resulted in the determination of high-resolution space use by birds carrying the loggers. Although these devices were large on the studied black-tailed gulls (*Larus crassirostris*) that carried them (i.e. 4.8–6.9% of their body mass), an absence of similar approaches in our literature search was not clearly explained by device mass (or size) limitations since devices with similar capabilities are available now at markedly reduced mass (e.g. PathTrack nanoFix GEO+RF GPS transmitter tags of approx. 2.6 g). We could envisage simultaneous deployments as per Tanigaki *et al.* [130] of both GPS and video loggers on an urban species such as a black-tailed gull that would meet the 5% body mass threshold for deployment of devices adhered to by many bird tracking researchers [131].

Beyond movement ecology, biologging offers a critical tool for addressing pressing urban bird conservation challenges, such as mortality and disease transmission. For instance, high-resolution tracking can help to identify collision hotspots for window strikes—a major urban threat responsible for close to one billion avian deaths annually in the United States alone [132]. By mapping fine-scale flight paths in relation to glass infrastructure, researchers can move beyond broad estimates to pinpoint which architectural features or urban corridors pose the highest risk. Similarly, tracking urban-adapted species is vital for monitoring the spread of zoonotic diseases like highly pathogenic avian influenza. Since cities act as hubs for both high-density human populations and mobile avian vectors, movement data are essential for modelling the interface where populations of wild and domestic bird species and humans overlap [133]. Biologging may also provide an objective measure of urban greening success. As cities invest in nature-based solutions and green corridors to bolster biodiversity [134], tracking data can confirm whether these spaces facilitate functional connectivity for native species or merely serve as ecological traps [132]. Integrating these applied outcomes will ensure that urban movement research translates into tangible improvements for both avian welfare and public health.

Finally, we argue that information derived from instances where biologging of urban bird movements has been attempted, but seen limited success, can be just as valuable as information published regarding successful attempts in advancing the field. A good example is that of Cope *et al.* [135] who documented difficulties in deploying GPS biologgers on little corellas (*Cacatua sanguinea*). Birds were able to remove harnesses very quickly after attachment not only from themselves but also from conspecifics. Such information is invaluable at the planning stage of tracking studies, and we argue that any difficulties faced, even in ‘successful’ studies, should be thoroughly documented and reported to assist in the generation of future knowledge.

5. Conclusions

Studies employing biologging technologies on birds in urban areas have already revealed much new information about their movements within and across these landscapes. That said, we have also highlighted the extent of remaining urban research that must be conducted as the world continues to urbanize and the impacts of humans on urban wildlife intensify as a result. Despite taxonomic and geographical biases in the scientific literature, we draw some potentially important conclusions from its synthesis. Indeed, it seems that some existing measures of urban tolerance are reasonably good at determining which species’ movements will be more impacted by urbanization. However, we argue that they should not be considered solely when determining the most vulnerable and important taxa to study using tracking biologgers. While we recognize that field studies are relatively more difficult and resource-heavy compared with desk-based ones, we argue that they have never been as important as now as a research priority because of the rapid pace of global urbanization.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The dataset of metadata gathered from published literature included in our review is available from the Dryad digital repository [136].

Supplementary material is available online at <https://doi.org/10.6084/m9.figshare.32262420>.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

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editing; T.J.M.: methodology, supervision, writing—review and editing; L.J.G.: methodology, supervision, writing—review and editing; S.J.R.: conceptualization, methodology, project administration, supervision, writing—review and editing.

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Conflict of interest declaration. We declare we have no competing interests.

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