


Community science data suggest the most common raptors (Accipitridae) in urban centres are smaller, habitat-generalist species

DANIEL S. COOPER,^{*1,2}  ALLISON J. SHULTZ,^{2,3} ÇAĞAN H. ŞEKERCIOĞLU,^{4,5} FIONA M. OSBORN¹ & DANIEL T. BLUMSTEIN¹

¹Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA

²Ornithology Department, Natural History Museum of Los Angeles County, Los Angeles, CA, USA

³Urban Nature Research Center, Natural History Museum of Los Angeles County, Los Angeles, CA, USA

⁴School of Biological Sciences, University of Utah, Salt Lake City, UT, USA

⁵Department of Molecular Biology and Genetics, Koç University, Istanbul, Turkey

As the world becomes more urbanized, identifying traits that allow some species to thrive in cities will be key to predicting which species will probably remain common and which may require conservation attention. Large, diverse, widely distributed and readily documented raptors represent an ideal taxonomic group to understand how species persist and thrive in urban areas. Global community science datasets can reveal patterns that might be obscured in studies limited to a small number of locations, those relying on presence/absence data or those conducted by a small number of observers. We analysed 127 species of raptors (hawks and related species; Family: Accipitridae) using recent community-science (eBird) records from 59 cities on five continents, modelling two indices of occurrence with five ecological and life history traits, and incorporating phylogenetic relatedness. Based on previous studies of avian traits in urban vs. rural populations, and well as our casual observations of birds in cities across the USA and around the world, we hypothesized that urban raptor communities would be dominated by smaller, ecological-generalist species regardless of the regional species pool. We defined urban occurrence in two ways: urban *abundance* (the frequency of breeding season reports within 10 km of a city centre) and species *proportion* (the relative abundance of each species in the local raptor community). We did not detect a strong phylogenetic signal for either urban occurrence index, suggesting that various unrelated raptor species may become common in cities of the world. In the best-performing models, both urban indices were significantly negatively associated with body mass, and significantly positively associated with habitat breadth; species proportion was also significantly associated with nest substrate breadth. Our analysis suggests that there may be an 'archetypal urban raptor' and that species lacking these traits (e.g. large, specialist taxa) may be at greater conservation risk as global urbanization increases.

Keywords: avian ecology, cities, eBird, generalist, global, hawks, ornithology.

Diurnal raptors (Family Accipitridae, including eagles, hawks, kites and related species) exhibit a variety of sizes and morphological traits, contain species ranging from diminutive sparrowhawks (*Accipiter* spp.) to massive Old World vultures

(*Gyps* spp.) and occupy a broad range of ecological niches on every continent except Antarctica. Many raptor species are clearly thriving in urban landscapes, nesting in built structures and planted introduced trees, feeding on human-subsidized urban prey and providing predation ecosystem services (Şekercioğlu 2006, McCabe *et al.* 2018, Rosenfield *et al.* 2018, Mak *et al.* 2021). Other

*Corresponding author.

Email: dan@cooperecological.com

species are restricted to wildland habitats, and for many tropical species and single-island endemics, their biology is comparatively poorly known (McClure *et al.* 2018, Buechley *et al.* 2019). While studies of wildland raptor communities (e.g. Marti *et al.* 1993) have long outnumbered those investigating urban ones, as the footprint of global urbanization expands (Seto *et al.* 2011), many raptors will need to adapt to some level of human disturbance to survive. Those species that are less tolerant of disturbance might be assigned a higher priority for conservation, as their populations will receive increasing pressure from the effects of expanding urbanization.

Many studies have investigated ecological traits associated with urban life in birds (see reviews by Chace & Walsh 2006, Marzluff 2016), but the few that have examined raptors explicitly have focused on single species or single cities (e.g. Cade *et al.* 1996; Kopij 2018; White *et al.* 2018, but see Kettel *et al.* 2018). Boal (2018) analysed eight traits associated with raptor occurrence in 14 US state capitals (all with human populations > 100 000), finding that both diet breadth and preferred 'normal' (non-urban) habitat type were strong predictors of presence in urban areas during both winter and summer. Yet this study was limited to the USA, and did not take species' abundance into account.

Prey type and availability are understood to be key to the development and maintenance of raptor communities, including those along an urban gradient (e.g. Rullman & Marzluff 2014). Estes and Mannan (2003) found stark differences in prey type in a study of urban vs. rural-nesting Cooper's Hawks *Accipiter cooperii* in Tucson, AZ, USA, with urban birds more restricted in their feeding (mainly doves, vs. a wide range of prey types). Yet these patterns may not be universal, as Suri *et al.* (2017) found no change in diet breadth or prey composition with increasing urban cover in a study of Black Sparrowhawks *Accipiter melanoleucus* around Cape Town, South Africa. Still, having a broad diet may enable bird species to thrive in urban areas, as suggested in a recent review of several hundred taxa (Palacio, 2020).

Prey type may favour certain traits in raptors in urban areas, including migratory status and body mass, but the direction may vary based on the type of urbanized habitat, the regional (raptor) species pool and the particular prey base. Powers (1996) suggested that sedentariness in an urban

Sharp-shinned Hawk *Accipiter striatus* was related to the year-round availability of this food source in Idaho, USA. Rullman and Marzluff (2014) linked raptor abundance in urbanized habitats to higher densities of urban prey – particularly rodents and birds associated with humans – than those found in wildland areas. Thus, in cases where the most common urban prey items tend to be small (compared with the available range of prey items consumed by raptors outside urban areas), raptor species associated with those cities might also be small. These patterns may vary based on local practices, such as the provisioning of 'predictable anthropogenic food subsidies' (Shochat 2004, Oro *et al.* 2013), which may in turn affect predator body size, but in a direction depending on the particular food resource. For example, larger sizes of urban carnivorous mammals have been documented in parts of Israel that receive a 'garbage subsidy' unavailable to non-urban populations (Yom-Tov 2003), and large garbage dumps within urban areas may have enabled massive Old World Vultures to persist in cities of Africa and India. Yet this may come with a serious cost associated with garbage, namely poisoning (see Cuthbert *et al.* 2011), which may then drive down the size of urban raptors in those cities. Rodenticide use may also influence raptor body size, in that species that primarily consume rodents may decline due to poisoning (Nakayama *et al.* 2019), whereas those that can shift to a 'safer' food item (such as birds) might be smaller raptor species buffered from its effects. Other costs associated with urban life could more directly reduce body size, such as increased parasite load in urban-dwelling raptors affecting nestling growth (Boal *et al.* 1998).

Morphological traits may also play a role in allowing birds to thrive in urban areas. Change in body size has been found to be associated with urban occurrence in mammals (e.g. Santini *et al.* 2019) but, for birds, this link is less clear, as is its ecological and evolutionary advantage (see Croci *et al.* 2008, Sol *et al.* 2014). Evans *et al.* (2009) found no significant size difference between urban and rural European Blackbirds *Turdus merula*, yet Meillère *et al.* (2015) reported smaller body size and reduced juvenile fat scores in urban-dwelling vs. rural House Sparrows *Passer domesticus*, and Caizergues *et al.* (2018) reported that urban Great Tits *Parus major* had shorter tarsus, lower body mass, and smaller wing and tail lengths relative to body mass. Comparing multispecies assemblages of

urban-associated birds with those in a larger 'regional species pool', Hensley *et al.* (2019) found no association with body mass in the urban species. Yet for raptors, White *et al.* (2018) found the largest species in Reno, Nevada (USA), Golden Eagle *Aquila chrysaetos*, to be the least tolerant of urban land use there, and found the two smallest hawks (both Accipiters) among the most urban-tolerant at various landscape scales of eight taxa examined. In a recent analysis of a raptor community around Los Angeles, California (USA), Cooper *et al.* (2020a) showed that as the region urbanized over five decades, nests of one smaller raptor, the Cooper's Hawk, had greatly increased in number, whereas the largest diurnal raptor (Golden Eagle) had vanished. However, small size does not guarantee urban adaptation; Cooper *et al.* (2020a) also found that the smallest raptors in their study area (White-tailed Kite *Elanus leucurus* and American Kestrel *Falco sparverius*) had also become extirpated, or nearly so.

Based on these previous studies, as well as our own field observations, we speculated that the most common nesting raptors in cities around the world may have a particular array of shared traits, including small size, broad diet (e.g. birds and mammals, including non-native, urban-associated prey items), sedentary (vs. migratory) populations, and a tendency to utilize a variety of habitats. Using sightings from birders and casual observers around the world entered into the community-science platform eBird (www.ebird.org), we identify breeding-season records of raptors in and around cities of various sizes and settings. We calculated urban occurrence in two ways for each focal species, and modelled these values using five morphological and ecological traits, along with phylogenetic data, to explore the characteristics of an 'archetypal urban raptor' – one that benefits from a predictable set of life history characteristics to thrive in urban environments. Not only would this identify a suite of traits that might confer success with future urbanization, it could, conversely, highlight species that may be at conservation risk (i.e. those that lack these urban-associated traits).

METHODS

Data preparation

We used GBIF (GBIF 2020a) to download sightings of hawks (Family Accipitridae, here referred

to as 'raptors') from the eBird Observational Dataset (an edited, simplified version of the complete eBird database; see Auer *et al.* 2020) hosted by GBIF from nine countries encompassing a range of global biomes (USA, Mexico, Colombia, Brazil, Spain, UK, South Africa, India and Australia) within a recent 5-year time period (2014–2018; GBIF 2020b, 2020c, 2020d, 2020e, 2020f, 2020g, 2020h, 2020i, 2020j, 2020k, 2020l; see Supporting Information Table S1 for the list of cities and Table S2 for the raptor species evaluated). We selected countries with a high number of sightings during the study period (2014–2018) submitted to eBird, and attempted to include a broad range of geography and ecological variation, while recognizing that certain biomes would necessarily be excluded due to lower rates of participation in eBird (e.g. equatorial Africa, southeast Asia). To maximize the diversity of species analysed, we did not select adjacent countries where the overlap in breeding species was likely to be very high (e.g. Canada and the USA). We selected a subset of records to include only the months when our target species would probably be breeding, which varied by country. We then selected the largest urban areas within each country based on the total population of the largest cities (generally population > 1 million). This was done to maximize the number of raptor records in a framework where we had no control over effort (mean = 6045 raptor records/city, range 28–38 881; mean = 13.4 species/city, range 3–24). We assumed that these cities, while not representative of every global biome, adequately represent a broad subset of ecological and biogeographical attributes found globally.

For each city, we visually estimated the 'urban centre' (i.e. the centre of the urban extent of each city) using the most recent aerial imagery on the Apple Maps application on the iPhone (ver. 14.2). We then used the Geosphere package (Hijmans *et al.* 2015) in R (R Core Team 2020; version 4.0.0) to find records at two radial distances: a 10-km radial distance, which we considered the 'urban core', and a 10- to 50-km radial distance, which we considered the 'peri-urban band'. See Supporting Information Figure S1 for aerial imagery of example cities, and Table S1 for a list of the coordinates used.

For landcover data, we used satellite imagery data (300 m resolution) from the Copernicus Climate Change Service Climate Data Store (2021)

Table 1. Urban index variables used to calculate raptor occurrence in urban areas.

Index	Measures	Calculation
Urban abundance	Numerical abundance of each species in urban core.	Density (n /terrestrial land area) of eBird reports within 10 km of urban centre.
Species proportion	Relative abundance of each species in urban core.	Percentage of eBird reports of given species relative to the number of reports of other raptor species, within 10 km of urban centre.

to examine land cover types surrounding our study areas. Using ESRI ArcMap 10.8 equipped with a spatial analyst licence, we converted the Copernicus NetCDF file into a raster format. From there, we created 10- and 50-km buffers around our coordinate points and used the *tabulate area* tool to calculate the total area of each land cover type within the specified buffer zone. We simplified the classifications into five major categories – cropland, tree cover, shrub/grasslands, urban areas and water features – and converted the values into percentages, which we used to calculate amounts of each land cover category within the 10-km urban core, and the 10- to 50-km peri-urban band. For each species found within 50 km of a particular city, we calculated a rate of detection in both the urban core and the peri-urban band by dividing the number of records by the amount of terrestrial habitat within each (i.e. the number of records divided by the non-water area in each).

To avoid overlapping data, we dropped overlapping large cities, opting to retain whichever was the larger one (e.g. San Jose, California, was retained over San Francisco, California). We recognize that the urban core may also include a mix of agricultural lands and fragments of scrub and forest, depending on the city, but confirmed that the urban core consistently had a higher amount of urban cover than the peri-urban band (71% urban cover; range 20–100% in urban core, vs. 12% urban cover; range 0–48% in peri-urban band; $n = 59$). Our final dataset of 127 focal species found within 50 km of the urban centre of at least one focal city represents about 45% of the world's 285 widely recognized raptor (Accipitridae) species and 67% of Accipitridae genera (45 of 67; Del Hoyo *et al.* 2013, BirdLife International 2019). This represented the 'species pool', from which we derived urban abundance and species proportion values (measured within the 10-km radial band) used in the analysis (several of which had

values at or near zero; see Table S2 for a complete list of species and values).

Measuring urban occurrence

We used two indices of occurrence to assess the presence of raptors in urban areas: urban abundance (number of records within 10 km of the urban centre) and species proportion (percentage of records of each species within 10 km of the urban centre; Table 1). Although several species consistently rank highly in each metric (e.g. the Shikra *Accipiter badius*), we believe that both metrics are useful to express a species' urban association, as the number of records varies widely by species and by city for a given species. Because we treated georeferenced records of individual birds, rather than nests, we did not attempt to estimate land cover surrounding the locations, with the assumption that many of the raptors used would have been observed in flight, and not necessarily associated with the habitat where the observer was standing (locations of nests would have been preferable, but a comparable global dataset of nests does not exist).

Traits

We evaluated traits most likely to influence urban occurrence based on previous research on urban birds, and urban raptors in particular (e.g. Samia *et al.* 2015, Boal 2018, Cooper *et al.* 2020b, Table 2). Trait values were taken from 'BirdBase', a dataset maintained and continuously updated by Şekercioğlu (Şekercioğlu *et al.* 2004, 2019), which we cross-referenced using additional sources (including Ferguson-Lees & Christie 2001 and Globalraptors.org 2020) to insert estimated values where needed due to missing data (see Supporting Information Table S3). Due to high collinearity between artificial nest substrate and nest substrate

Table 2. The traits used in our analyses. Body mass, diet breadth, habitat breadth and nest substrate values were taken from Ç. H. Şekercioğlu (unpubl. data). Migratory status values were inferred from descriptions in Ferguson-Lees and Christie (2001). Various sources were used to fill in missing values (e.g. Globalraptors.org 2020).

Variable	Type	Description
Body mass	Numeric; grams	Ln transformed; up to four reported values (various sources) were averaged.
Diet breadth	Numeric; 1–6	Calculated from nine major food categories: invertebrate, fruit, nectar, seeds, land vertebrates, fish, carcasses/garbage, vegetation and miscellaneous items.
Habitat breadth	Numeric; 1–10	Calculated from 15 major habitat types: forest, bamboo, dry forest/woodland, shrubland, savannah, grassland, dry/open, rocky areas, desert/dunes, agricultural/artificial, sea coast, riparian, wetland, pelagic and 'other'.
Nest substrate breadth	Numeric; 1–6	Calculated from 12 categories: bamboo, building, stump, ground, cactus, invertebrate nest, pole, rock, shrub, tree, water and grass.
Migratory status	Factor; 1–3	Defined as fully migratory: (1) vacating most of breeding range during the non-breeding season; (2) partially migratory: engaging in short-distance movements during non-breeding season, facultatively migratory and/or nomadic; (3) largely sedentary/non-migratory throughout the year.

breadth ($r > 0.6$) using Spearman's rank correlation, we eliminated the former, both because its correlation with urban occurrence is already well established (e.g. Cooper *et al.* 2020b) and because substrate breadth seemed more informative for a wider range of species (few species we analysed are known to nest on artificial structures). Ultimately, we selected five trait variables for the models: mass, diet breadth, habitat breadth, migratory status and nest substrate breadth (see Supporting Information Figure S2 for a correlation matrix of urban indices and traits).

Statistical analysis

To account for phylogenetic relatedness among species in our analyses, we used the latest phylogeny of Accipitridae from the Open Tree of Life (2019, ver. 3.1), which represents a synthetic tree derived from multiple sources of phylogenetic information. We first tested for phylogenetic signal in each urban index individually by fitting a series of generalized least squares (GLS) models (without trait variables) that employed three different modes of evolution: Brownian motion (BM), Pagel's lambda, Ornstein–Uhlenbeck (OU) and a non-phylogenetic model. This phylogenetically informed GLS (PGLS) framework is useful for data where the dependent variable lacks a normal distribution (Münkemüller *et al.* 2012).

For the Brownian motion, or random-walk, model we used a Blomberg's K test (Blomberg *et al.* 2003), which compares the variance of phylogenetically independent contrasts with what we

would expect under a BM model. Here, $K = 1$ means that relatives resemble one another as much as we should expect under BM (i.e. non-relatedness), $K < 1$ means that there is less phylogenetic signal than expected under BM, and $K > 1$ means that there is more. For Pagel's lambda (Pagel 1999), if our estimated lambda = 0, then the traits would be inferred to have no phylogenetic signal. Lambda = 1 corresponds to a BM model, and $0 < \text{lambda} < 1$ is intermediate. The OU mode of evolution incorporates 'stabilizing selection' wherein the trait is drawn toward a fitness optimum, or long-term mean, rather than being completely random and directionless (Martins 1994). This model has two terms: alpha, which represents the strength of the pull toward the fitness optimum (where alpha = 0 indicates no pull, as in a BM model, the larger the alpha value, the stronger the pull), and sigma², which is the dispersion of the data (Martins 1994). Finally, to test for no phylogenetic signal, we used a 'no-signal' GLS model where lambda was set to 0. We used the *phytools* package in R (ver. 0.7-70; Revell 2012) for the BM, Pagel's lambda and OU models, and the *nlme* package in R (ver. 3.1-147; Pinheiro *et al.* 2019) for one non-phylogenetic general linear model, and compared adjusted Akaike information criterion (AICc) values of each to select the model that best explained variation in the data.

We repeated this process to test associations separately between each urban index and the five traits, using the same three phylogenetic models and one non-phylogenetic model described above.

Table 3. Comparison of the phylogenetical signal of each of the two urban indices alone, using three modes of evolution (BM, OU, Pagel's lambda) and one non-phylogenetically informed model. Models with the lowest AICc values for each index are in bold.

	K	Sigma squared	Alpha	Lambda	AICc
Index: urban abundance					
BM	0.0357, $P = 0.190$	9.589	2.718	0.0110; $P = 0.721$	290.121
OU					259.835
Pagel's lambda		0.190	187.849		
Non-phylogenetic			184.770		
Index: species proportion					
BM	0.0233, $P = 0.057$	0.274	2.718	0.730; $P = 0.008$	-161.251
OU					-191.749
Pagel's lambda		0.00587	-250.802		
Non-phylogenetic			-257.418		

For each analysis, best-fit parameters of the phylogenetic model were estimated with maximum likelihood. Lastly, we selected the analysis with the lowest AIC values as the best model for each urban index tested, and compared correlations using that model.

We checked residuals from the full models using QQ tests, finding a somewhat skewed pattern for both urban occurrence indices (Supporting Information Figures S3 and S4). However, this pattern was not changed by log-transforming the dependent variables, and probably reflects 'reality', in that many raptor species are simply rare in urban areas. We intentionally assembled a large sample size of cities and species to improve model performance (see discussion in Mundry 2014).

RESULTS

Modelling the urban occurrence indices alone (urban abundance and species proportion) without the life history or environmental variables, we found little evidence of phylogenetic signal for either (Table 3). While this suggests that phylogeny alone is unrelated to urban occurrence, we still incorporated phylogenetic relatedness into modelling the indices using the five trait variables. In doing so, we found the OU, Pagel's lambda and non-phylogenetic models returned similarly low AIC values for each index, again suggesting little phylogenetic signal in the data for models incorporating phylogeny (Table 4). We found two variables significantly associated with both urban abundance and species proportion: body mass (negative) and habitat breadth (positive; Table 5). Additionally, we found that nest substrate breadth was significantly positively associated with species

Table 4. Comparison of the AIC scores of four models used to test two urban indices against five traits (see Table 2). The lowest scores for each variable are indicated in bold text. Note that the scores of OU, Pagel's lambda and the non-phylogenetic model are all very close for each index, suggesting minimal influence of phylogeny in explaining variation.

Model	Urban abundance	Species proportion
BM	348.295	-68.744
OU	216.170	-207.407
Pagel's lambda	213.115	-208.281
Non-phylogenetic	214.188	-209.407

proportion. This suggests that both smaller raptor species and habitat generalist species were more abundant in the urban core of the cities examined, and were more relatively dominant in their local raptor communities. Neither urban index was found to be significantly correlated with diet breadth or migratory status.

The most common urban species (Fig. 1a) and dominant species (Fig. 1b) appear to fall within a fairly narrow window of body mass (150–1000 g), with those at the extreme ends of body mass having lower values for the two urban occurrence indices. Considering that most of the 127 raptor species are rather rare in the urban core of cities (Table S2), the most abundant/dominant urban species globally represent a handful of smaller (but not the smallest) species that have managed to achieve abundance in many cities, such as Red-tailed Hawk *Buteo jamaicensis*, Black Kite *Milvus migrans* and Roadside Hawk *Rupornis magnirostris*. Several of these same species were among those with the highest habitat breadth values, including Red-tailed Hawk, Black Kite and Brown Goshawk *Accipiter fasciatus* (Fig. 2).

Table 5. Results from the best model for each urban index using generalized least squares tests, fitted to explain variation based on the five traits analysed. *Values significant at $P < 0.05$.

Variable	Value	95% CI	P
Urban abundance (Pagel's lambda)			
(Intercept)	0.390	[-0.153 to 0.933]	0.158
log(Mass)	-0.105	[-0.185 to -0.025]	0.010*
Diet breadth	-0.022	[-0.102 to 0.057]	0.578
Habitat breadth	0.146	[0.086–0.205]	0.000*
Nest substrate breadth	0.110	[0.004–0.146]	0.043*
Migratory status (Partial/Sedentary)	-0.125	[-0.479 to 0.228]	0.483
Migratory status (Fully/Sedentary)	-0.132	[-0.455 to 0.192]	0.422
Species proportion (Non-phylogenetic)			
(Intercept)	0.139	[0.030–0.139]	0.013
log(Mass)	-0.026	[-0.041 to 0.011]	0.001*
Diet breadth	0.001	[-0.013 to 0.015]	0.891
Habitat breadth	0.018	[0.007–0.028]	0.001*
Nest substrate breadth	0.011	[-0.007 to 0.030]	0.229
Migratory status (Partial/Sedentary)	0.009	[-0.053 to 0.071]	0.783
Migratory status (Fully/Sedentary)	0.001	[-0.057 to 0.059]	0.973

Yet, counter-examples abound, including several small raptors found to have little to no representation in the urban core (see Table S2; e.g. Rufous-thighed Kite *Harpagus diodon*, Gabar Goshawk *Micronisus gabar*, Bicoloured Hawk *Accipiter bicolor* and Little Sparrowhawk *Accipiter minullus*), as well as raptors with high habitat breadth values that were rare in the urban areas studied (e.g. Bonelli's Eagle *Aquila fasciata* and *Buteogallus* spp.). Several common urban raptors were found to have fairly low habitat breadth, including Cooper's Hawk, Red-shouldered Hawk *Buteo lineatus* and Eurasian Sparrowhawk *Accipiter nisus*. While a few common urban species were somewhat large-bodied (e.g. *Buteo* spp.), none was larger than Red-tailed Hawk, a mid-sized raptor (Fig. 1).

DISCUSSION

Raptors are well established in urban areas throughout the world, and the literature on their ability to adapt to our human-centred environment continues to expand (e.g. Mak *et al.* 2021). The lack of phylogenetic signal in our urban occurrence indices suggests that a variety of unrelated raptor taxa are able to thrive in cities, a result evident in the broad range of hawk genera found most commonly in the world's urban areas. So, while several are in the genus *Accipiter*, there appears to be no single taxonomic group of raptors found most commonly in urban areas globally. In many cities

of India and Australia, for example, this role appears to be filled by members of the genus *Accipiter* (Shikra and Brown Goshawk, respectively), whereas in many Latin American cities, two unrelated, non-*Accipiter* species, Grey Hawk *Buteo plagiatus* and Roadside Hawk, are the most common and/or dominant raptor. Perhaps not coincidentally, these latter two species happen to resemble most species of *Accipiter*, being smallish species with greyish and brownish plumage, a banded tail and rapid wingbeats – characters, we suggest, of an 'archetypal urban raptor'.

The significant positive associations we found with habitat breadth and nest substrate breadth suggest that the most common raptors in urban areas, both in absolute numbers (urban abundance) and in relative abundance (species proportion), are generalists – utilizing a variety of vegetation and terrain types for both foraging (habitat breadth) and breeding (nest substrate breadth). These associations reflect previous findings that generalists thrive in cities, whereas urban-avoiders show a narrower habitat tolerance (Crocini *et al.* 2008, Sol *et al.* 2014). Multiple studies over decades have documented the utilization of habitats in and around urban areas by the same urban raptors we found to be most common where patches of woodland and other habitat elements persist in urban areas (e.g. Stout *et al.* 2006 for Red-tailed Hawks, Kumar *et al.* 2014 for Black Kites, and Rosenfield *et al.* 2018 for Cooper's Hawks). Urban habitat use of tropical raptors has

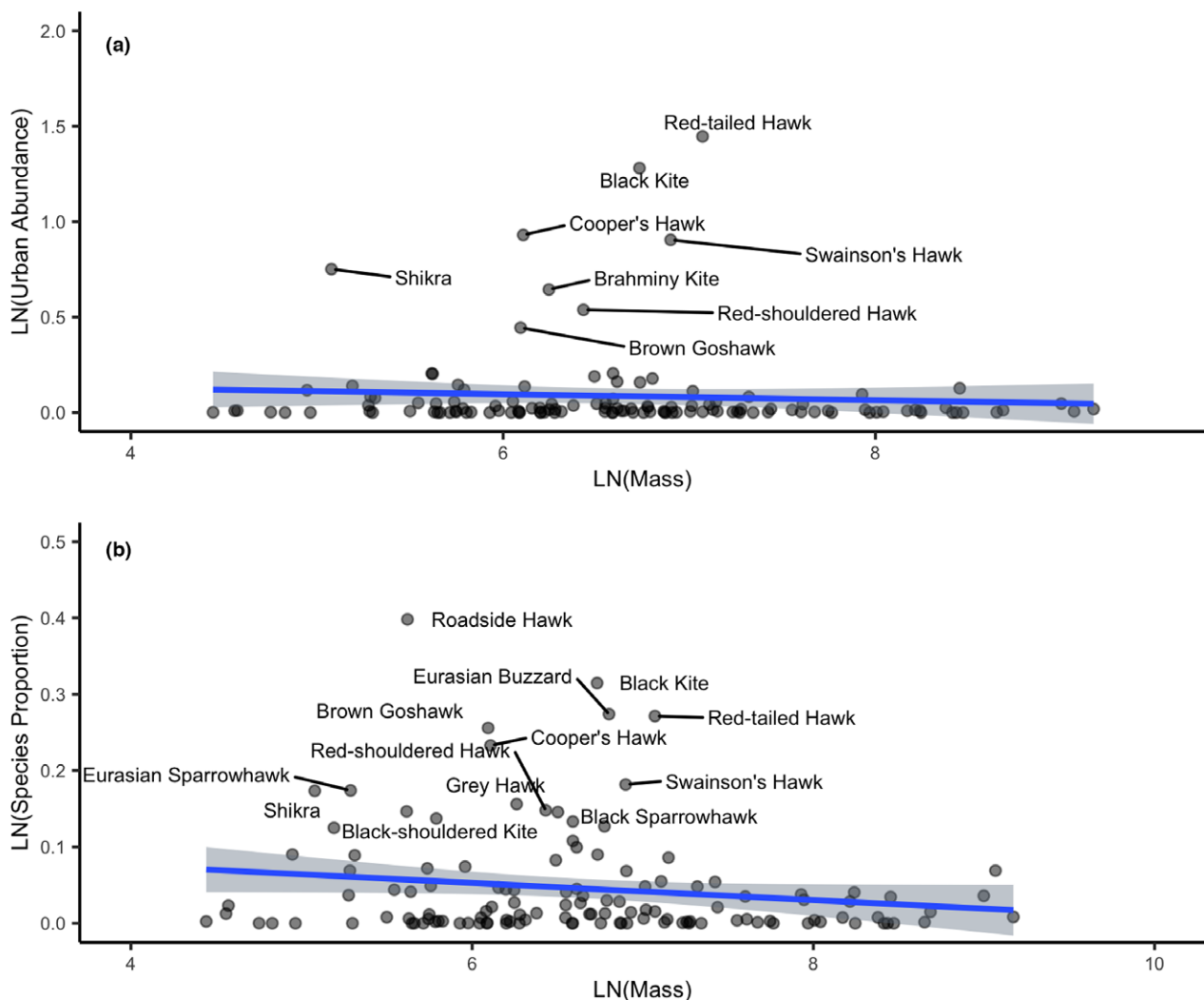


Figure 1. Small to mid-sized species are among the most abundant (a) and dominant (b) of 127 focal raptor species across 59 cities. Mean body mass is plotted on a natural log scale, and a value of 7 roughly corresponds to 1 kg. The most abundant and dominant species are labelled, and the grey shading indicates a 95% CI. [Colour figure can be viewed at wileyonlinelibrary.com]

received far less attention, but we note a survey of Brown Goshawk in Darwin, Australia (Riddell 2015), and mentions of urban occurrence of Shikra in Singapore (Ward 1968) and Brahminy Kite *Haliastur indus* in Java (Van Balen *et al.* 1993). A few urban-associated, habitat-generalist species that were not among the most abundant species in our dataset include several that are restricted to tropical and subtropical areas, where eBird use is lower. Their use of urban habitats has received scant research attention, but we note previous studies of urban occurrence of Roadside Hawk (Dos Santos & Rosado 2009) and Ovambo

Sparrowhawk *Accipiter ovampensis* (McPherson *et al.* 2021).

Raptor species scoring highly in urban occurrence with *low* habitat breadth values, such as Eurasian Sparrowhawk and Red-shouldered Hawk, may be utilizing some particular habitat present in urban areas, such as a localized or super-abundant food source (see Bell *et al.* 2010) or the presence of an appealing microhabitat such as riparian woodland (see Preston *et al.* 1989). While body mass is fairly straightforward to measure, a potential difficulty in interpreting trait breadth as a variable is that it does not distinguish between a

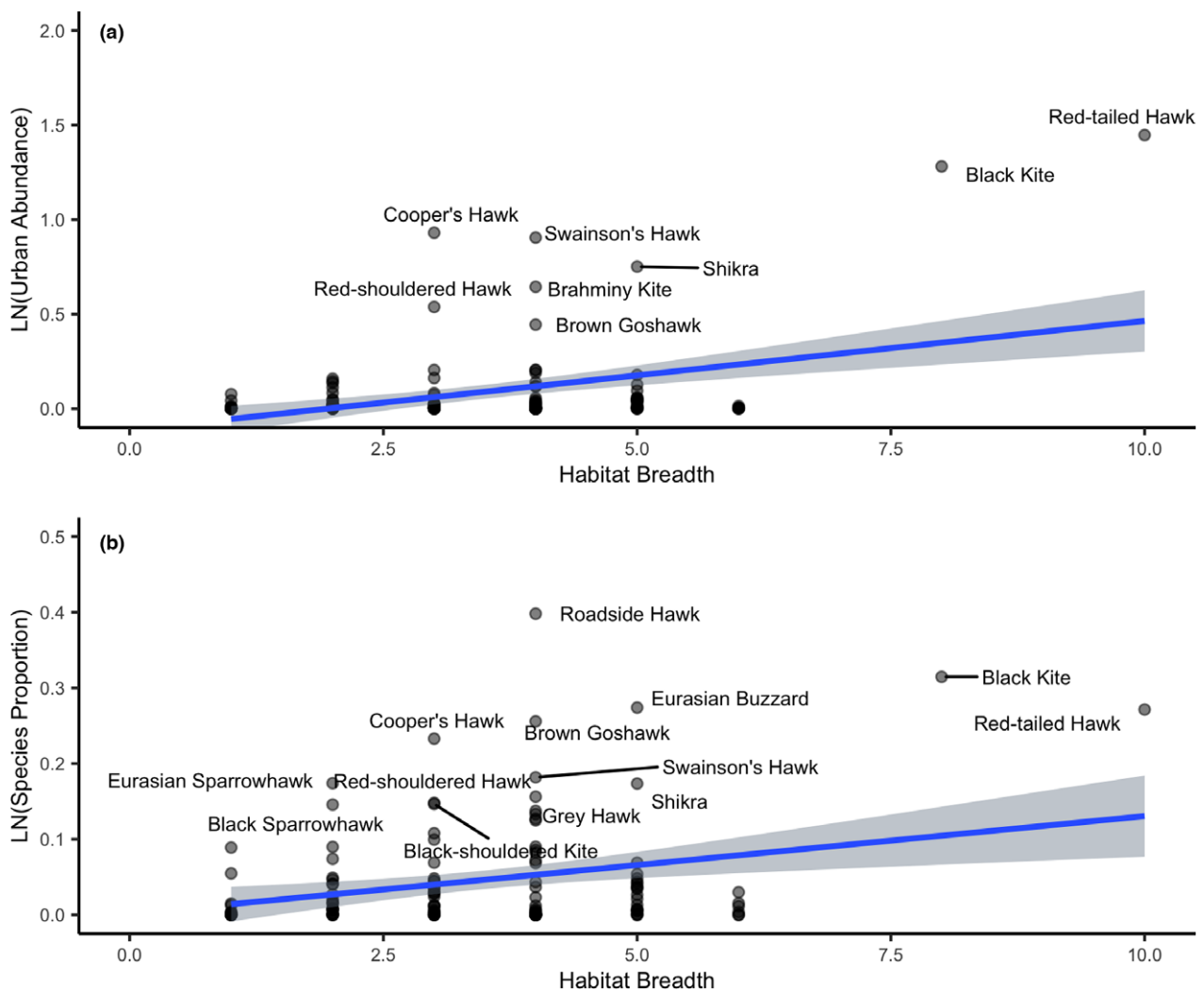


Figure 2. Both species abundance (a) and species dominance (b) in urban areas are positively associated with habitat breadth, based on 127 focal raptor species across 59 cities. The most abundant and dominant species are labelled, and the grey shading indicates a 95% CI. [Colour figure can be viewed at wileyonlinelibrary.com]

species that is ubiquitous and flexible, and one that requires a diversity of a particular resource, such as a mosaic of multiple habitat types (or prey types). More granular investigation into actual habitat usage by urban raptors within urban areas (particularly in the tropics) would elucidate some of these patterns, given how variable habitats can be from city to city (see Dykstra 2018 for discussion). Understanding what allows for the persistence of these species, and large-yet-urban-tolerant raptors such as Red-tailed Hawk, in urban areas could guide conservation decisions in cities working to promote a diversity of raptors.

Further research into the rarest smaller and mid-sized raptors in the study may yield important information about why certain (smaller) taxa are threatened by urbanization, as our results suggest these would be more common (see Poos & Jackson 2012). It could also elucidate why the largest raptors appear to be absent or very rare in urban areas (Fig. 1). Is this simply because more small raptors are abundant (everywhere) than large ones, or might there be a mechanistic explanation for having a small body size in an urban area? Several authors have identified a decline in body mass over time linked to climatic warming (e.g. Lurgi *et al.* 2012,

Weeks *et al.* 2019, but see Salewski *et al.* 2014), and Merckx *et al.* (2018) suggested that because urban areas are influenced by the heat island effect, smaller body size in animals favours species with increased dispersal capability and reduced metabolic needs. While most raptors would be adept at dispersal, it seems logical that the high mobility of smaller species such as Accipiters and similar genera makes them 'pre-adapted' to urban life (see Johnson & Munshi-South 2017). Future work could investigate the relationship between urban occurrence and other aspects of body size such as wing loading, and the role of types of flight or foraging methods conducive to life in urban areas.

Further work could also investigate inter- and intra-species effects and competition, as the presence of particular species in a given raptor community could affect which other species are excluded or included via competition. Perhaps the sheer abundance of the most common species in a given region might enable them to find mates readily and thus occupy a broader geographical area (including urban areas) than a scarce species would, regardless of their preferred habitat type or body size. This spillover effect into the city from peripheral areas could be examined by comparing species' abundance in the peri-urban band around cities with that within the urban core.

Community science datasets can reveal patterns that might be obscured by studies limited to a small number of locations, or those using a simple binary classification of occurrence such as range maps or presence/absence (Adler *et al.* 2020). Nevertheless, as a source of data, we recognize that eBird reports have potential limitations that could not be totally controlled in our study, including observer bias (over-reporting the same individual, under-reporting a familiar species due to its abundance, or overlooking a shy or inconspicuous species). We deliberately selected countries with high levels of eBird participation, and analysed multiple cities from each country to maximize occurrences of each species in an effort to reduce this bias. Future investigations could always use more cities and more species, as the popularity of online community-science platforms such as eBird and iNaturalist (www.inaturalist.org) grows. Still, although these platforms are excellent for determining seasonal status and distribution (and are comparable to existing standardized survey methods; see Horns *et al.* 2018 and Neate-Clegg

et al. 2020), they cannot be used for assessing demographics or nesting success. Increased participation in eBird across all countries outside the USA and Canada, particularly in urban areas, would refine future analyses, as would a comparison with patterns found in winter raptor communities in cities, though this may be unlikely to change overall results, as most raptors are non-migratory (Horns & Şekercioğlu 2018; Ç. H. Şekercioğlu unpubl. data).

We caution against equating urban occurrence of any wildlife species (including urban raptors; see Dwyer *et al.* 2008) with conservation success. Sol *et al.* (2020) and Bregman *et al.* (2016) discuss the loss of functional diversity in urban species assemblages, which in the long term may lead to the loss of global biodiversity as particularly specialist species fail to adapt faster than their habitats are urbanized (Şekercioğlu 2011). Consequently, the selection pressure toward generalist bird species in urban areas means that most of the threatened and near-threatened raptor species may not survive in these human-dominated landscapes. Furthermore, our study did not compare the traits of individuals within the same species (where, for example, smaller individuals of the same species might have reduced fitness; see Liker *et al.* 2008). Thus, we cannot draw any conclusions about the long-term outlook for the population health or productivity of urban raptors through this analysis. Repeating the study for other taxonomic groups (including non-avian taxa) would be worthwhile to test whether the patterns observed for raptors are universal. Finally, more research into the mechanisms affecting raptor occurrence in urban areas, incorporating diet studies, nest-searching and monitoring, and demographic research (such as nesting success) would help fill the gaps in our knowledge of urban wildlife and allow better planning for future ecological changes.

We thank Dan Chamberlain, Richard Fuller, David Douglas and three anonymous reviewers for insightful edits that greatly improved the manuscript. The Blumstein lab (in particular, Rachel Blakey and Watcharapong 'Win' Hongjamrasslip) and Ryan Harrigan at UCLA assisted Cooper in analytical methods, and members of the Urban Nature Research Center at the Natural History Museum of Los Angeles County (including Kayce Bell, Adam Clause, Greg Pauly and Jann Vendetti) provided helpful editorial comments on earlier drafts. We would like to thank the Cornell Lab of Ornithology and the thousands of eBird participants around the world

who continue to improve the database through their sightings and volunteer review process. This study was funded in part by the UCLA Grand Challenge as part of Daniel S. Cooper's doctorate programme.

FUNDING

None.

ETHICAL NOTE

None.

AUTHOR CONTRIBUTIONS

Daniel S. Cooper: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (supporting); Supervision (lead); Writing – original draft (lead); Writing – review & editing (lead). **Allison J. Shultz:** Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Writing – review & editing (supporting). **Cagan H. Sekercioglu:** Data curation (equal); Writing – review & editing (supporting). **Fiona M. Osborn:** Formal analysis (supporting); Methodology (supporting); Software (supporting). **Daniel T. Blumstein:** Supervision (lead); Writing – review & editing (supporting).

Data availability statement

The authors confirm that the data supporting the findings of this study are available within the Appendix S1 associated with this paper, and via download from Auer *et al.* (2020).

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Received 3 February 2021;
Revision 3 December 2021;
revision accepted 18 January 2022.
Associate Editor: David Douglas.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Cities used, including coordinates used for urban centre and months used for breeding season records (2014–2018).

Table S2. Summary of focal species and trait values, averaged across the number of cities recorded. DB—Diet Breadth; HB—Habitat Breadth; Mass—body mass; Mig.—Migratory status, SBS—Number of nest substrate categories, Urb_Abund—Urban Abundance, Urb_Prop—Urban Proportion. Refer to Table 2 for descriptions of trait variables.

Table S3. Summary of edits to eBird records and trait database (Şekercioğlu *et al.* 2004, including updates). These include values found in existing sources (e.g. Ferguson-Lees & Christie 2001), and those estimated from similar species to replace missing data (e.g. body mass for similarly sized

species). We also report taxa dropped due to nomenclatural and spelling discrepancies between the various databases and R packages used to help guide future investigators. Finally, we list the taxa omitted from analysis in the particular countries or cities where they are unlikely to be breeding in any of our focal cities (in some cases omitting them from the entire analysis if occurring only as non-breeding visitors; e.g. *Buteo lagopus*).

Figure S1. (a) Aerial imagery of 10- and 50-km radial bands around cities of Spain used in analysis. (b) Aerial imagery of Barcelona, Spain, showing amount of urbanized land within 10- and 50-km radial bands. Note that urban cover in this particular city is fairly dispersed, such that areas of urban and wildland cover are located both within the 10-km band and within the ‘peri-urban’ band. (c) Aerial imagery of Ahmadedabad, India, showing solid urbanization within urban core of city (10-km radial band) and comparatively little urban cover in the ‘peri-urban’ band. (d) Aerial imagery of Sao Paulo, Brazil, showing how the urban core extends well outside the 10-km radial band, but the ‘peri-urban’ band is still far less developed than the urban core.

Figure S2. Correlation matrix of variables used in the study using Spearman’s rank correlation.

Figure S3. QQ plot of residuals for the best-performing model using Urban Abundance as the dependent variable (Pagel’s lamdba).

Figure S4. QQ plot of residuals for the best-performing model using Species Proportion as the dependent variable (Non-phylogenetic).