



Living in the city: can anyone become an 'urban exploiter'?

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ABSTRACT

Aim As urban landscapes expand, shifts in biodiversity are occurring. This is leading biogeographers and ecologists to consider human-dominated landscapes in their current work. One question that arises is: what characterizes those species that are widespread in the most highly urban environments compared with those restricted to less urbanized areas in the city? Here, we aim to identify the traits that enable species to become urban exploiters, i.e. to dominate highly urbanized surroundings. Identifying these traits may help us better predict and possibly mitigate the biotic homogenization occurring in these areas.

Location Israel in general, with special focus on the city of Jerusalem.

Methods Combining literature and field-based data for birds in Israel we compared phenotypic, behavioural and life-history traits between urban exploiters and urban adapters. The latter occur in urban landscapes, but are characteristic of the less urbanized parts of the city. We then examined the trends along a finer field-sampled gradient of increasing urbanization from sub-natural to downtown areas within the city of Jerusalem.

Results Urban exploiters and adapters differed primarily in social structure and migratory status: exploiters were significantly more social and sedentary than urban adapters. Clear trends were also seen for dietary preferences along a gradient of increasing urbanization in Jerusalem, such that, with increasing urbanization, the proportion of granivorous species increased whereas the proportion of species feeding on invertebrates declined. In contrast, neither relative brain size nor behavioural flexibility, as measured by feeding innovations, differed significantly among urban exploiters and adapters in Israel or along the urbanization gradient in Jerusalem specifically.

Main conclusions The results of our study suggest that being successful in more vs. less urbanized environments in the city is not necessarily a factor of brain size nor of how flexible and behaviourally innovative the species is; rather, it depends on a combination of traits, including diet, degree of sociality, sedentariness and preferred nesting sites.

Keywords

Birds, brain size, Jerusalem, sociality, urban adapters, urban exploiters, urban gradient.

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INTRODUCTION

Approximately half of the human population currently live in cities, with the proportion of those residing in urban environments increasing rapidly, especially in the developing

world (United Nations, 2005). By 2030, the global urban population is predicted to reach 5 billion people (United Nations, 2005). As cities expand, natural habitats are lost and fragmented, and native biodiversity often declines (Marzluff, 2001; Miller & Hobbs, 2002). This has been a central focus of

recent studies considering human-dominated landscapes by biogeographers and ecologists (e.g. Jokimäki *et al.*, 1996; Ricketts *et al.*, 2001).

Research on biodiversity in urban landscapes, and especially on urban birds, has shown that the richness of species along a gradient of increasing urbanization tends to decline with increasing urbanization (Marzluff, 2001; Shochat, 2004; Faeth *et al.*, 2005; Clergeau *et al.*, 2006; McKinney, 2006). Several studies have shown that richness peaks in areas of intermediate urbanization (Blair, 1996, 1999; Crooks *et al.*, 2004; see also Shochat *et al.*, 2006). Blair (1996), in his pivotal Northern California study, divided the bird community along an increasing urbanization gradient into categories. The gradient extended from relatively undisturbed areas outside the city to the downtown city core. In areas with native vegetation, the community was dominated by what he termed 'urban avoiders'. These were native species that occurred almost exclusively in these areas. In environments with intermediate levels of urbanization, 'suburban adapters' were the predominant community. These species included both native and non-native species. In the most urbanized areas, where buildings and pavement cover increased, this dominance shifted towards a small number of species, mainly non-native ones, that Blair termed 'urban exploiters'. These species were later defined by Shochat *et al.* (2006, p. 186) as 'species thriving as urban commensals to the point that they become dependent on urban resources'. In these heavily urbanized areas, the native habitat was highly disrupted and there were very few local native species (see also Jokimäki & Suhonen, 1998; Melles *et al.*, 2003).

The pattern in which a small number of species that are well adapted to human-dominated landscapes (urban exploiters) replace a wider range of native species is repeated in many regions all over the world, and has been termed biotic homogenization (Blair, 2001a; Lockwood & McKinney, 2002; Crooks *et al.*, 2004). The formation of uniform urban communities is caused by the transformation of landscapes to urban environments and the creation of similar ecological structures in different areas (Blair, 2001b). A possible explanation for the shift in dominance is that some species, namely the urban avoiders, do not adapt (or are not pre-adapted) to the changes to their natural habitat caused by intense urbanization (Blair, 1996; McKinney, 2002). On the other hand, some species may take advantage of the fact that the avoiders do not enter the highly urbanized parts of the city. These urban species are 'experts' in exploiting the environmental changes caused by urbanization (Blair, 1996). Thus, the degree of expertise in exploiting urban environments is positively correlated with the degree of urbanization (Blair, 1996).

In view of this, it is important to understand what enables some bird species to live in the most intensely urbanized environments, while others are excluded. In other words, what turns a bird species into an urban exploiter? Among the traits that have been proposed as enabling species to persist in highly urbanized surroundings are their ability to live and forage

without fear in the vicinity of humans (i.e. commensalism), the ability to exploit human-related resources (e.g. garbage dumps, feeders, nesting boxes) (Chace & Walsh, 2006), low resource investment in territory maintenance, gregarious behaviour (Mills *et al.*, 1989), and sedentariness (Jokimäki & Suhonen, 1998; Chace & Walsh, 2006). Differences in nesting and feeding may also play a role in urban exploitation and adaptation (Chace & Walsh, 2006).

Although all of these traits have been implicated in the success of urban species, an additional trait, namely behavioural flexibility, may also play a significant role. In order to survive under the non-natural conditions of the city, species living in such environments should adopt new feeding techniques and feed on novel food items. One measure of behavioural flexibility that has received considerable attention is the number of feeding innovations (Lefebvre *et al.*, 1997, 1998; Nicolakakis & Lefebvre, 2000). A feeding innovation is a feeding or foraging behaviour observed or reported for the first time, for example a house sparrow (*Passer domesticus*) using an automatic sensor to open a bus station door (see Lefebvre *et al.*, 1997 for more examples). More innovative species are generally better at problem solving and learning in complex surroundings (Timmermans *et al.*, 2000; Webster & Lefebvre, 2001), an ability that may further help them adjust to the urban environment.

In addition to these traits, relative brain size may also vary with urban invasion/exploitation. It has recently been shown that birds with larger brains tend to establish themselves in novel environments more successfully than those with smaller brains (Sol *et al.*, 2005a). Relative brain size covaries with several traits such that species that are sedentary (Sol *et al.*, 2005b), are more behaviourally flexible (Lefebvre *et al.*, 2002) and are more likely to be successful invaders (Sol *et al.*, 2002) tend to have relatively large brains. Here, we hypothesize that a combination of several traits, including relatively large brains, will be present in urban exploiters, enabling them to persist in the city centre in both the native and alien range.

In this study we aimed to identify and examine the differences between urban exploiters and adapters. While a variety of bird species occur in human-dominated landscapes, only a few manage to exploit successfully the most highly urbanized areas. We first compared behavioural, morphological and life-history traits in two groups of urban birds – urban exploiters vs. adapters from Israel, using a literature-based categorization. We then examined trait shifts in birds along a detailed gradient sampled from downtown to sub-natural locations of decreasing urbanization within the city of Jerusalem.

More specifically, we made the following hypotheses.

1. *Diet*: Urban exploiters will tend to be omnivores, granivores, or aerial insectivores, whereas there will be a larger percentage of non-aerial insectivores and frugivores among the adapters (Adams, 1994; Blair, 1996; Jokimäki & Suhonen, 1998).

2. *Sociality*: Urban exploiters will be more gregarious than adapters, because such behaviour makes it easier to forage in

dense urban surroundings (Coleman & Mellgren, 1994). Gregarious species may also have an advantage in areas where roost sites are limited (Jokimäki & Suhonen, 1998) and where food is clustered, enabling information to be transferred in roost sites.

3. *Migration status*: Urban exploiters will tend to be sedentary species that can maintain their nesting sites from year to year, while migrants will tend to avoid the most urbanized locations within the city.

4. *Breeding location*: Urban exploiters will nest mainly in cavities and in buildings, while adapters will tend to nest in trees and bushes.

5. *Behavioural flexibility and feeding innovations*: Urban exploiters will have relatively bigger brains than adapters. Accordingly, the degree of behavioural flexibility and number of feeding innovations (reflecting behavioural flexibility) of exploiter species are expected to be higher than those of adapters.

METHODS

Categorization of Israel's bird species into 'urban exploiters' and 'urban adapters' was carried out following the definitions given by Blair (1996). The main difference is that what Blair termed suburban adapters we here call urban adapters. In referring to exploiters we refer to those species that are most tightly dependent and are most successful in the most highly human-dominated (i.e. downtown) urban areas. Other species found in the city are defined as adapters. We surveyed the literature on the birds of Israel and based our categorization mainly on Paz & Eshbol (1990) and Shirihi (1996).

Field-based categories

In order to validate the literature-based definitions, we examined whether the literature-based exploiters are indeed the most common in the most highly urbanized environments. We compared the literature survey with field data collected in Jerusalem. Species seen in large numbers in the most highly urbanized downtown commercial areas were defined as urban exploiters.

During August–October 2003, we surveyed bird species in 40 locations representing a range of urban environments within the city. The gradient consisted of four predefined environment types within the city. These were: (1) the downtown region, a commercial area that is highly built up and paved and has very little vegetation; (2) residential neighbourhoods; (3) urban parks, usually located within the residential regions, all of which are managed and irrigated; and (4) sub-natural areas within the city, which are less managed. Each of these habitat types was sampled in such a way that they were repeated at different distances from the city periphery. Residential areas were located in six neighbourhoods and sampling was carried out in all cases in a secondary street of a similar width at a predetermined distance from the nearest intersection of roads. To account for the high heterogeneity

among the different sub-natural areas, we sampled a range of open bathas and fields, semi-woodlands with scattered shrubs, and denser woodlands. Owing to differences in the degree of spatial heterogeneity among sites, the sample sizes were not equal. Five of the locations sampled were in the downtown business district, nine were residential, 11 were urban parks, and 15 were sub-natural habitats (two open-area habitats, five dense tree habitats, and eight habitats of semi-woodland and scattered scrub). We compared means and proportions for traits among the four environments.

Each location was visited twice a week through the survey period: in the first 4 h following sunrise and 3 h prior to sunset, coinciding with peak bird activity (the total number of surveys was 329). The bird point-count surveys were carried out following Buckland *et al.* (2001). Each location was divided into five concentric rings of 10-m radius from 0 to 50 m. In addition, a 50-m and onward interval was set. Before beginning the survey at each point, the sampler waited at the point for 10 min, which served as a 'calming period'. A 10-min sampling period followed, in which the sampler noted all birds either heard or seen and the distance belt in which they were observed.

Literature-based analysis

Behavioural and life-history traits

Data regarding species' traits were taken from the literature (Cramp & Simmons, 1980; Hollom *et al.*, 1988; Paz & Eshbol, 1990; Shirihi, 1996; Del Hoyo *et al.*, 1999; Iwaniuk & Nelson, 2003; E. Banker, unpublished data) (Table 1). Traits included (1) diet (divided into seed eaters, fruit eaters, invertebrate eaters, vertebrate eaters, and omnivores, eating all of the above items); (2) migratory status (sedentary or migrating in Israel, or both, i.e. sedentary only in some parts of the region); (3) sexual and seasonal dimorphism; (4) social structure (or flocking potential – foraging and roosting in solitude, pairs, small groups of up to 10 birds, or flocks of 10 or more individuals); (5) mating habits (socially monogamous or polygamous); (6) territoriality; (7) nesting density (scattered nests located > 50 m apart [no colonies], loose breeding colonies with a few dozens of metres between nests, and dense colonies, where nests are located very close, up to several metres, to each other); (8) nesting site; (9) nest building (which sex builds the nest); (10) incubation (which sex incubates the eggs); (11) incubation (average number of days according to the literature); (12) average clutch size; (13) nesting cycles (average number of cycles per year); (14) developmental state at hatching according to Starck & Ricklefs (1998), namely altricial (incapable of moving around on its own soon after hatching), semi-altricial, semi-precocial and precocial (capable of moving around on its own soon after hatching); and (15) fledging (the average number of days from laying to fledging according to the literature). For further information on these categories, see http://www.stanford.edu/group/stanfordbirds/text/essays/Precocial_and_Altricial.html.

Table 1 A list of the behavioural and life-history traits collated for the urban species examined, based on the literature (see text for more information)

Trait	Definition
Diet	Seeds, fruit, invertebrates, vertebrates or omnivorous.
Migratory status	Sedentary or migratory
Sexual dimorphism	Yes, slight or none
Seasonal dimorphism	Yes, slight or none
Social structure	Solitary, pairs, small groups (< 10 birds), large groups (> 10 birds)
Mating habits	Monogamous or polygamous
Territoriality	Yes or no
Nesting density	Scattered (> 50 m apart), loose colonies (12–50 m apart), dense colonies (< 12 m apart)
Nesting site	Cavity, tree, bush, rock or ground
Nest building	Male or female
Incubation behaviour	Male or female
Incubation period	Average number of days from last day of laying to hatching
Nesting cycles	Average number of nesting cycles per year
Clutch size	Average number of eggs per clutch
Developmental mode	Developmental state at hatching: altricial, semi-altricial, semi-precocial or precocial
Fledging age	Average number of days from hatching until young leave the nest
Brain size	Average brain volume of each species in mL
Feeding innovations	Number of reports of feeding innovations relative to the total number of published reports for each taxonomic group (see Lefebvre <i>et al.</i> , 1997)

For those traits with multiple categories (e.g. nest site, diet), species were classified as being in more than one category where appropriate. With respect to diet, any species that fed on all four food categories was classified separately as omnivorous. Where there was variation in a trait throughout a species distribution, the dominant trait or behaviour present in the Israel population was used. Thus, if a species had both sedentary and migratory populations, but the population in Israel was migratory, it was classified as migratory.

Neuroanatomical and feeding innovation data

Relative brain sizes were obtained from Iwaniuk & Nelson (2003). The data base contains data on body mass and brain volume (endocranial volumes) for 19 species recorded in the literature survey (see Appendix 1). Details of the measuring methods are provided in Iwaniuk & Nelson (2001, 2002). The use of endocranial volumes has been demonstrated to yield estimates that are not significantly different from actual brain masses (Iwaniuk & Nelson, 2002). For eight additional species, we obtained data concerning brain volume from other sources (Ebinger & Lohmer, 1984; Mli'kovsky', 1989a,b,c,d).

We extracted data on feeding innovations from studies by Lefebvre and colleagues (Lefebvre *et al.*, 1997, 2002; Nicolakakis & Lefebvre, 2000; Timmermans *et al.*, 2000; Sol *et al.*, 2002). Specifically, we were interested in determining if the exploiters have higher innovation rates than the adapters. Each species was therefore scored as having high, average or low innovation rates based upon histograms presented in Lefebvre *et al.* (2001) and Timmermans *et al.* (2000). Innovation rates in these histograms are expressed as the residuals from a linear regression of the number of feeding innovation reports against the total number of papers published for each taxonomic group, and therefore account for possible differences in research effort. Because specific innovation reports were lacking for 20 of the 49 species examined, the analyses of innovation rates were performed on parvorder/infracorder means derived from figures in Lefebvre *et al.* (2001) and Timmermans *et al.* (2000).

Jerusalem bird traits

For the Jerusalem birds, which were analysed in detail along a gradient of increasing urbanization within the city, we selected for comparison a series of breeding, social structure, feeding, and life-history traits. We examined and compared these traits in detail among species in the four different environments. Traits were collated from several sources, including Cramp & Simmons (1980), Paz & Eshbol (1990), Shirihai (1996), Svensson *et al.* (2003), and E. Banker (unpublished data). To estimate breeding location, we examined whether the species was a cavity nester (this included cavities in trees, rocks, the ground and buildings), or whether it occupied an open nest (including on a tree, bush, rock or the ground). A single species can belong to more than one category, but this is rare. We examined their diet based on the categories given above. Feeding items were categorized to seeds, fruit, invertebrates and vertebrates. Species can feed on items from more than one category, and so can be included in several food-type categories. Species that are known in Israel to feed on all food-type categories were included as omnivores. We classified the migration status based on the dominant migration status characteristic of the Jerusalem region population when data were available. When unavailable for the region, we based the classification on data known for the majority of the species' population in Israel, according to Shirihai (1996). In cases where a species has several different breeding populations (e.g. the Eurasian sparrowhawk), we used the category that most of the populations in Israel follow. We used the categories all-year resident, summering (breeding in the region), wintering (non-breeding), and migrant (pass through) species.

In addition to these traits, we classified species as to whether they were 'range expanders' or not. Range expanders were defined as species that have recently expanded their distributional range as a result of human-related factors (e.g. urbanization). This classification was based on Hatzofe & Yom-Tov (2002).

We classified the social structure of the species during feeding in the non-breeding season. We used information for the species in the study region of Jerusalem, and, when unavailable, in Israel in general. Social structure was categorized into single, pairs, small flocks (3–5 individuals), medium flocks (6–14 individuals) and large flocks (15+ individuals). We also noted the whole range of social structures during the non-breeding season for those species (e.g. the barn swallow) in which social structure in the region is variable. The social structure of many of the migrant species during active migration while they pass through the region can vary considerably from single to large flocks and can change substantially during the migration season. Flocks during this season may therefore represent individuals moving together, but not forming a flock as in highly social species.

Statistical analyses

Literature-based analyses

Chi-square tests were used to test for significance in differences between adapters and exploiters for all categorical data. For the remaining continuous traits (e.g. incubation period), we performed two-tailed *t*-tests to test for differences between adapters and exploiters. Some traits, such as brain volume, incubation period and fledging age, are significantly correlated with body mass. We therefore tested whether each of the continuous traits was significantly correlated with body mass using least-squares linear regressions of the log-transformed traits. Where significant correlations were present, *t*-tests were performed on the residuals from these linear regressions. The statistical significance was estimated following a Bonferroni correction (Rice, 1989; Palmer, 1994).

Field data – Jerusalem birds

To test for statistical significance between the field data and species traits, we used Kendall's τ -test, a non-parametric test for correlation (Sokal & Rohlf, 2000).

RESULTS

The literature-based categorization of Israeli bird species to exploiters based on Paz & Eshbol (1990) and Shirihi (1996) returned five species in this category (Appendix 1): the house sparrow (*Passer domesticus*), hooded crow (*Corvus corone*), feral pigeon (*Columba livia*), palm dove (*Streptopelia senegalensis*), and common swift (*Apus apus*).

Field sampling in Jerusalem strongly supported this categorization. Four of these five bird species classified as urban exploiters based on the literature were the only birds sampled in all five downtown locations in Jerusalem. These included the hooded crow, house sparrow, feral pigeon and palm dove. All these species also occurred in relatively large numbers in other urban areas in the city and were present in most sites sampled within the city. The hooded crow was present in 97.5% of the

40 locations studied in Jerusalem, and the house sparrow was present in 95% of locations. The feral pigeon and palm dove were both present in 85% of the 40 locations. These species were observed in large numbers along the entire range of the urbanization gradient, and were the only ones sampled in the most urban areas within the city.

The main deviation between the fieldwork and the literature was for the common swift, which was included as an urban exploiter based on the literature, but was not observed in the field surveys. The common swift is a passage migrant and a common summering species in Israel, and is observed between late winter (February) and summer. Because the surveys were carried out during late summer and autumn, the lack of common swifts in the surveys is unsurprising.

COMPARISON OF EXPLOITERS AND ADAPTERS

Literature-based analyses

Life-history traits

There were significantly more exploiters than adapters that formed flocks (Table 2). Similarly, significantly more exploiters than adapters nested in colonies or loose colonies (Table 2). Thus, it appears that exploiters are significantly more social than adapters. The other life-history traits surveyed exhibited no significant difference between adapters and exploiters in Israel (Table 2). Four of the five exploiters are sedentary, the exception being the common swift. Although the majority of the adapters are at least partially migratory (8/14), no significant difference in migratory behaviour was present between adapters and exploiters. The mating system was uniformly monogamous. There was no significant differ-

Table 2 Results of statistical tests of life-history traits on those species described as urban exploiters and adapters in the literature (see Appendix 1)

Trait	Statistic	df	P
Flocking	$\chi^2 = 4.94$	1	≤ 0.05
Colonial nesting	$\chi^2 = 6.11$	1	≤ 0.03
Migratory	$\chi^2 = 2.04$	1	≤ 0.20
Territorial	$\chi^2 = 0.22$	1	≤ 1.0
Sexually dimorphic	$\chi^2 = 0.03$	1	≤ 1.0
Seasonally dimorphic	$\chi^2 = 0.42$	1	≤ 1.0
Cavity nester	$\chi^2 = 0.01$	1	≤ 1.0
Altricial	$\chi^2 = 1.27$	1	≤ 1.0
Both sexes construct nest	$\chi^2 = 2.04$	1	≤ 0.20
Granivorous	$\chi^2 = 2.54$	1	≤ 0.20
Insectivorous	$\chi^2 = 3.97$	1	≤ 0.05
Omnivorous	$\chi^2 = 0.65$	1	≤ 1.0
Nest cycles	$t = -0.86$	17	0.40
Clutch size	$t = 1.67$	17	0.11
Incubation period	$t = 1.24$	14	0.24
Fledging	$t = 0.06$	14	0.96
Brain volume	$t = 1.73$	14	0.11

ence in the number of species that were territorial, sexually dimorphic, seasonally dimorphic, cavity nesters, altricial or where both sexes constructed the nest (Table 2). Among the dietary categories, there were not significantly more exploiters than adapters in the granivores or omnivores category (Table 2). There were, however, significantly more adapters than exploiters feeding on invertebrates. When the analyses were constrained to strict insectivores, this significant effect was lost ($\chi^2 = 0.42$, $df = 1$, $P \leq 1.0$). Among the continuous variables, there was no significant difference between exploiters and adapters in the number of nest cycles per year or clutch size (Table 2). Similarly, after correcting for body mass, no significant differences in incubation period or age at fledging were detected (Table 2).

Neuroanatomical and feeding innovations

After correcting for body mass, no significant difference in brain volume was detected between exploiters and adapters (Table 2). The species representation within both the exploiters and the adapters included members of orders and sub-orders with both relatively large (e.g. Corvida, Psittaciformes) and small (e.g. Columbiformes) brains. A similar pattern was observed with mean innovation rates. Most of the adapters (73%) were from orders and sub-orders with average innovation rates. Half of the exploiters were from orders and sub-orders with average innovation rates (50%). There was little difference in the percentage of species from groups with high innovation rates between the adapters (15%) and exploiters (17%).

Field-based analyses

Overall, 40 bird species were seen in Jerusalem during the course of the field sampling. All species sampled elsewhere in the city were also sampled in the sub-natural locations, where the total number of species was also 40 (Table 3). Therefore, we also compared the results for the birds sampled only in the sub-natural locations.

Jerusalem birds – trait shifts along an urban to sub-natural gradient

Diet, sociality, sedentariness, range expansion and nesting site were all significantly correlated with the degree of urbanization of the four environment types (Table 4), and corroborated our comparison of exploiters and adapters. Feeding characteristics showed clear trends when moving from the most to the least urbanized areas within the city (Table 4). While 100% of the species occurring in the downtown region included seeds in their diet, there was a gradual decline to 40% for the species occurring in the sub-natural areas within the city. When this figure was calculated for the 11 species occurring exclusively in the sub-natural locations, it declined to 18% (Table 4). A gradual decline also appeared for the fruit eaters (Table 4). However, an opposite trend was seen for invertebrate eaters.

While all species that occurred in the sub-natural locations alone ($n = 11$) preyed on invertebrates, there was a gradual decrease to 67% of the species in the downtown region. The proportion of omnivores declined from 50% of the downtown birds to zero for the birds occurring exclusively in the sub-natural areas (Table 4).

There was a clear difference in social structure between the downtown species and those in all other locations in the city. All downtown species form flocks larger than a pair (though the palm dove is often also seen in singles or in pairs), while only about half of the species in the three other areas (residential, urban parks and sub-natural) form flocks regularly (Table 4). From the downtown to the sub-natural areas, there was a significant increase in the proportion of species that have a solitary social feeding structure during the non-breeding season (Table 4).

Migration characteristics also showed clear trends along the urbanization gradient. While all of the bird species occurring in the downtown region were all-year residents, this percentage declined gradually towards the sub-natural areas, where 55% were residents. Furthermore, only 36% of the bird species occurring only in the sub-natural locations were all-year residents (Table 4).

The majority of the downtown species have undergone recent range expansion in Israel. Significantly more species that expanded their ranges were found in more urbanized habitats. Only one of the 11 species recorded in the sub-natural areas alone was a recent range expander (possibly a locally introduced population from the Jerusalem Zoo, S. Yedavab, personal communication).

Cavity nesting characteristics showed clear changes from the downtown to the sub-natural regions. While 50% of the species occurring in the downtown region were cavity nesters, only 18% of those seen exclusively in the sub-natural regions were cavity nesters (Table 4). However, the declining trend when moving along the urban gradient was less clear, with no significant differences between residential, urban park, and sub-natural areas. Open-nesting species included species with nests on trees, bushes, rocks (but not cavities) and the ground. While the proportion of bush and rock nesters declined from the downtown to the sub-natural regions, the proportion of ground nesters increased from none in the downtown birds to 18% for the birds seen in sub-natural areas only (Table 4).

Mean body size showed a significant trend of decline from downtown towards sub-natural areas. The largest mean body size was found in the downtown birds (243 g), which were on average more than double the size of the sub-natural birds, and 2.5 times larger than the average of the birds that occurred exclusively in sub-natural areas (Table 4).

Aside from the urban parks, a general decline in mean relative brain size occurred when moving from the downtown to the sub-natural areas (Table 4). However, the mean value for the urban parks birds was the highest of all regions, and was mainly caused by the addition of the Eurasian hobby (*Falco subbuteo*), which has one of the largest values and was

Table 3 Species occurrence (marked as 0 for absence or 1 for presence) in each of four area types sampled in Jerusalem, namely downtown locations, residential, urban parks and sub-natural areas

English name	Latin name	Downtown	Residential	Urban parks	Sub-natural
Eurasian sparrowhawk	<i>Accipiter nisus</i>	0	1	1	1
Common kestrel	<i>Falco tinnunculus</i>	0	1	1	1
Eurasian hobby	<i>Falco subbuteo</i>	0	0	1	1
Chukar partridge	<i>Alectoris chukar</i>	0	0	0	1
Spur-winged lapwing	<i>Vanellus spinosus</i>	0	0	0	1
Feral pigeon	<i>Columba livia</i>	1	1	1	1
Eurasian turtle dove	<i>Streptopelia turtur</i>	0	1	0	1
Palm (laughing) dove	<i>Streptopelia senegalensis</i>	1	1	1	1
Common swift	<i>Apus apus</i>	0	0	0	1
Eurasian hoopoe	<i>Upupa epops</i>	0	0	1	1
White-throated kingfisher	<i>Halcyon smyrnensis</i>	0	0	0	1
European bee-eater	<i>Merops apiaster</i>	0	1	1	1
Rose-ringed parakeet	<i>Psittacula krameri</i>	0	1	1	1
Syrian woodpecker	<i>Dendrocopos syriacus</i>	0	1	1	1
Barn swallow	<i>Hirundo rustica</i>	0	0	1	1
Spectacled bulbul	<i>Pycnonotus xanthopygos</i>	1	1	1	1
Common redstart	<i>Phoenicurus phoenicurus</i>	0	0	0	1
Whinchat	<i>Saxicola rubetra</i>	0	0	0	1
Common blackbird	<i>Turdus merula</i>	0	1	1	1
Blackcap	<i>Sylvia atricapilla</i>	0	0	0	1
Eastern orphean warbler	<i>Sylvia hortensis</i>	0	0	0	1
Lesser whitethroat	<i>Sylvia curruca</i>	0	0	1	1
Sardinian warbler	<i>Sylvia melanocephala</i>	0	1	1	1
Common whitethroat	<i>Sylvia communis</i>	0	0	0	1
Graceful prinia	<i>Prinia gracilis</i>	0	1	1	1
Eastern olivaceous warbler	<i>Hippolais pallida</i>	0	0	1	1
Willow warbler	<i>Phylloscopus trochilus</i>	0	0	1	1
Spotted flycatcher	<i>Muscicapa striata</i>	0	0	0	1
Great tit	<i>Parus major</i>	0	1	1	1
Red-backed shrike	<i>Lanius collurio</i>	0	0	1	1
Masked shrike	<i>Lanius nubicus</i>	0	1	1	1
Palestine sunbird	<i>Nectarinia osea</i>	0	1	1	1
Eurasian jay	<i>Garrulus glandarius</i>	0	1	1	1
Western jackdaw	<i>Corvus monedula</i>	1	0	1	1
Hooded crow	<i>Corvus corone cornix</i>	1	1	1	1
House sparrow	<i>Passer domesticus</i>	1	1	1	1
Common linnet	<i>Carduelis cannabina</i>	0	0	0	1
European goldfinch	<i>Carduelis carduelis</i>	0	1	1	1
European greenfinch	<i>Carduelis chloris</i>	0	1	1	1
Ortolan bunting	<i>Emberiza hortulana</i>	0	1	1	1

not seen in the downtown or residential areas (Table 3). The lowest values were seen for the birds that occurred only in sub-natural areas, many of which were passerines. The variation around these values is large in all area types.

When ranked on a scale from 3 (high innovation rate) to 1 (low innovation rate), there were no clear trends in the mean feeding innovation ranks of the birds along a gradient of decreasing urbanization within the city (Table 4). This may be related to the fact that the behavioural innovation data available were not fine enough to differ among the species, and most of the species are ranked as average in their innovation value. Finally, neither relative brain size nor mean feeding innovations varied much among the five habitats.

DISCUSSION

Based on this study, only a small proportion of the birds that are found in the city occur in the most highly urbanized environments (downtown business district). These urban exploiters contribute to a process similar to that seen in invasion biology, where a small number of species occur in a large number of highly human-dominated environments, leading to biotic homogenization (McKinney & Lockwood, 1999; McKinney, 2002; Clergeau *et al.*, 2006). Of the five urban exploiters included in this study only one species, the palm dove (*Streptopelia senegalensis*), was non-native, apparently brought to the region some time around the 18th century

Table 4 A summary of the distribution of the categorical traits and means of continuous traits among the habitat categories along the urban gradient in Jerusalem (downtown, residential areas, urban parks, sub-natural areas), as well as for birds sampled only in the sub-natural areas. For the categorical traits, the proportion of species that exhibited each trait is provided. Significant correlations are indicated as follows: * $P < 0.05$, ** $P < 0.01$.

	Region	Downtown	Residential	Urban parks	Sub-natural	Only sub-natural
Diet	Seeds**	1	0.62	0.46	0.4	0.18
	Fruit**	1	0.86	0.82	0.78	0.64
	Invertebrates**	0.67	0.81	0.89	0.9	1
	Vertebrates*	0.33	0.24	0.29	0.23	0.09
	Omnivores*	0.50	0.14	0.14	0.10	0
Dominant social structure	Single**	0	0.29	0.32	0.33	0.36
	Pairs	0	0.19	0.11	0.15	0.18
	Small flocks	0.33	0.24	0.29	0.28	0.27
	Medium flocks	0.17	0.19	0.18	0.15	0.09
	Large flocks	0.5	0.1	0.11	0.1	0.09
Dominant migration status	All flocks (without pairs)	1	0.52	0.57	0.53	0.45
	Non-resident (migrant, wintering, summering)**	0	0.24	0.36	0.45	0.64
	Resident year-round**	1	0.76	0.64	0.55	0.36
	Migrant (pass through)	0	0.05	0.21	0.25	0.36
	Summering*	0	0.14	0.11	0.18	0.27
Range expansion	Wintering	0	0.05	0.04	0.03	0
	Non-expanding**	0.33	0.62	0.68	0.75	0.91
Nesting	Recent range expander**	0.67	0.38	0.32	0.25	0.09
	Cavity nesting (all types)	0.50	0.33	0.36	0.30	0.18
Nesting	Open nest: tree	0.50	0.62	0.61	0.60	0.55
	Open nest: bush	0.67	0.52	0.50	0.53	0.55
	Open nest: rock**	0.17	0.05	0.04	0.03	0
	Open nest: ground	0	0	0	0.05	0.18
Mean body mass in g (\pm SD)†		243 \pm 197	136 \pm 141	115 \pm 130	114 \pm 144	96 \pm 188
Mean relative brain size (SD)†		0.032 \pm 0.22	0.022 \pm 0.17	0.039 \pm 0.14	0.0034 \pm 0.15	-0.054 \pm 0.12
Mean behavioural innovations (SD)‡		2.00 \pm 0.89	2.14 \pm 0.65	2.25 \pm 0.59	2.13 \pm 0.56	1.91 \pm 0.30
Number of species		6	21	28	40	11
Number of families		4	16	18	23	8
Number of species† (used in body-size and relative brain-size calculations)		5	16	22	31	8

†Full data for these traits were available for 31 of the 40 species.

‡Innovations were scored on a relative numerical scale of 1 (low), 2 (average) and 3 (high).

(Hatzofe, 2005). There are some discernible trends in our analyses and we review these by focusing on our initial hypotheses. We hypothesized that urban exploiters would differ from adapters in their diet (the exploiters tending to be omnivores, granivores and aerial insectivores), in their social structure (tending to be more gregarious), migration status (tending to be sedentary), and breeding locations (tending to nest in cavities), as well as in their brain size and behavioural flexibility, as estimated by the number of feeding innovations, which was expected to be higher in the exploiters. In partial support of our hypotheses, the urban exploiters tend to differ from adapters in their diet, sociality, sedentariness, and, to some extent, nesting site.

DIET AND URBAN EXPLOITERS

In the city of Jerusalem, diet plays a crucial role in determining where specific bird species may be found. Highly urbanized

areas inadvertently limit many bird species that have specific dietary needs. In agreement with findings of studies that sampled a gradient extending to outside the urban area (e.g. Clergeau *et al.*, 1998), seed and fruit eaters decrease and invertebrate (mainly insect) eaters increase from the most highly urbanized areas to the more sub-natural ones. Thus the most highly urban species are more likely to be granivores or omnivores than they are to be insectivores. This supports previous studies (Emlen, 1974; Beissinger & Osborne, 1982; Adams, 1994; Blair, 1996; Jokimäki & Suhonen, 1998), although ground insectivores have also been found in highly urban landscapes (McKinney, 2002; Chace & Walsh, 2006).

Within the downtown area, many species have resorted to scavenging on human refuse. This ability to adapt readily to new food sources enables these birds to exploit new niches within the urban complex. Indeed, the downtown area holds the highest percentage (50%) of omnivorous birds in relation to species in the other regions, while none of the 11 birds

occurring solely in the sub-natural areas are omnivores. Furthermore, two-thirds of species observed in the downtown locations are recent range expanders into human-dominated landscapes. These two patterns seem to go hand in hand. More generalist species may be better 'pre-adapted' to human environments, enabling them to persist over a wide range of areas within the city and to expand their range into diverse human-dominated landscapes that have increased in recent years.

Interestingly, recent research has shown that omnivorous species have an advantage mainly in temperate regions, where natural food resources are limited in the winter (Lim & Sodhi, 2004). Our study areas are mediterranean, where the winter is mild and is the rainy season, and where there are clear seasonal trends. These species obtain much of their food from non-natural sources, such as garbage, feeding tables, and other human-related resources that are present even during the winter and help the birds survive the harsh winter conditions. In tropical regions, there is no increase in the abundance of omnivorous species as the environment becomes more urban (Lim & Sodhi, 2004). The same could be true also for the seed eaters, because they, too, often feed on seeds and garbage from human sources.

URBAN EXPLOITERS – SOCIAL AND SEDENTARY

Sociality was also predicted to enable better urban exploitation and may help urban exploiters to persist in several ways. For example, foraging in groups improves the ability to locate and communicate about sources of food, to avoid predators, and to overcome competition (Sol, 2007). Social foraging, roosting and breeding may also enable species to locate food sources that are variable in time and space or that are highly patchy. Finally, living in social groups may improve the ability of a species to compete over food with other species and to deal with potential predators. Overall then, sociality may improve both survival in urbanized areas and the ability of a species to exploit the urban environment.

The proportion of species that are migratory steadily increased with decreasing urbanization, indicating that sedentariness is also an important factor determining whether a species exploits the urban environment. The ability to occupy and defend territories and foraging sites throughout the year is probably an important factor shaping success in the most highly urban areas. It may enable a species to successfully occupy new habitats. In addition, migratory birds may lose their nesting sites to competing sedentary bird species when they leave the city (Jokimäki & Suhonen, 1998). The only exception to this pattern within the urban environment is the common swift, which is a seasonal migrant in Jerusalem. As predicted, the ability of swifts to nest on buildings and to feed on aerial prey may allow them to take advantage of nesting sites and food items that are not used by other insectivore species in the downtown region.

NESTING IN THE CITY

Nesting site was also correlated with urban exploitation. Urban exploiters were significantly more likely to nest on rocks (e.g. buildings) than adapters. This may be the result of a number of factors, including the general lack of suitable trees for species that prefer to nest and feed in natural vegetation (Whitney & Adams, 1980; Lim & Sodhi, 2004). Because native vegetation is scarce in the most highly urbanized areas, many native species lack their natural nesting and roosting sites, food resources, or both. Dead trees are usually removed, and species that nest in dead trees are rarely seen in the dense city areas (Blair, 1996). The same is true for ground or shrub nesters, because humans or domesticated animals, such as cats and dogs, threaten them (Churcher & Lawton, 1987; Lim & Sodhi, 2004). In contrast, cliff or cavity nesters (e.g. the feral dove and house sparrow), as well as those that nest in open nests on rocks, can more often successfully exploit human surroundings in the form of buildings, especially tall ones for nesting (Beissinger & Osborne, 1982; Adams, 1994; Crooks *et al.*, 2004). Canopy nesters, such as the hooded crow, can also be found in highly urban environments but also in the more sub-natural areas (see also Lim & Sodhi, 2004).

For all of the remaining variables, no clear differences were present between adapters and exploiters or along our urban to sub-natural habitat gradient. Some of the lack of differentiation between exploiters and adapters could be attributable to the relatively small number of species that are exploiters. However, we did obtain significant differences between the exploiters and adapters for several traits, as discussed above. It is likely that many of the life-history traits exhibit a large amount of variation within both exploiters and adapters. In fact, this variability among species may enable more species to coexist in urban and suburban habitats.

Alternatively, some of these traits may not be those that are the most important in determining whether a species can adapt to or exploit the urban environment. For example, the brain is a heterogeneous organ that is the product of changes in multiple brain regions (Striedter, 2005). Therefore, relative brain size may not always be the best estimate for detecting and understanding what traits play an important role in species adaptation to a new environment (e.g. Iwaniuk & Nelson, 2001; Iwaniuk & Arnold, 2004), and correlations found may be difficult to interpret (Iwaniuk, 2004). Despite the strong correlations between brain size and behavioural flexibility (Lefebvre *et al.*, 1997, 2004), it is thus not that surprising that we failed to detect significant effects.

Some of the results may be explained by taxonomic effects, which are difficult to quantify and include in this study, given the relatively small sample sizes of urban exploiters. It is clear that certain families, such as the Columbidae, are more characteristic of the downtown and most urban areas, being urban exploiters, than others, such as the Sylviidae, which tend to avoid these sites and are more restricted to sub-natural areas within the city, being adapters. As species of the

same family often tend to show similar life-history, morphological and behavioural traits (Bennett & Owens, 2002), one may predict that this will have an effect on the results. However, it is important to mention that these species may also have a higher potential to compete over food, nesting sites and other resources, leading to niche separation. Thus statistical corrections for taxonomic effects are unlikely to solely explain the factors that enable one species rather than another to persist in different parts of the city under different levels of urbanization.

Finally, several traits that we examined do covary with one another. For example, altricial species tend to have longer incubation and fledgling periods, relatively larger brains, larger brood sizes, and different diets compared with other developmental-mode categories (Bennett & Owens, 2002; Iwaniuk & Nelson, 2003). Unfortunately, the small number of exploiters precluded the use of multivariate statistics, but it is possible that interactions between some traits may be significantly different between adapters and exploiters.

WHY ARE THERE SO FEW EXPLOITERS?

One hypothesis is that urban exploiters are highly successful in competing with the other species, excluding them from the most highly urbanized environment. On the other hand, it is possible that only these few species can actually exploit the resources found in this highly urbanized environment. This leads to the question whether the most urbanized environments are harsher or are actually more moderate for birds than other, more natural environments within and outside the city. The truth seems to lie somewhere between the two and to depend on the species in question (Chace & Walsh, 2006). For those species that are able to exploit a wide array of food items, that are flexible and innovative enough to develop the ability to exploit new resources, and that have co-evolved with humans (e.g. the hooded crow or the house sparrow), the city centre may be a haven. For many other species, however, the city centre is a poor environment, which they are unable to exploit successfully.

WHAT MAKES A SPECIES AN EXPLOITER?

The answer to the question what makes a species a successful urban exploiter appears to be based not on a single trait but rather on a combination of diet, sociality, sedentariness, preferred nesting sites and range expansion into human-dominated landscapes. That said, there is some variability in the traits. For example, the Common Swift is an insectivore and seasonal migrant, and is able to exploit the urban environment, whereas other species that have these traits cannot. Part of the reason for this variability may be the sequence in which species first invade the urban environment. For example, commensal and human-introduced species may be at a significant advantage over native species because of prior adaptation to environments that are modified by humans. If this is true, then what makes a species capable of

urban exploitation is not only a complex interaction of several different life-history traits, but also the interaction between these traits and humans, which in itself has important implications for understanding the historical and contemporary biogeography of urban species.

CONCLUSIONS

Based on our analyses, it is clear that a combination of life-history traits enables some bird species to become urban exploiters and to enter successfully the most urban environments and live in such areas all over the world. A more global analysis is required to assess the generality of these differences. From this study it appears that highly urbanized environments lead to a process similar to that in invasion biology, with a few species (some of which are also highly successful invaders) taking over this highly urban habitat and becoming very abundant (see also Clergeau *et al.*, 2006 and McKinney, 2006). These species tend to be highly social and sedentary. Therefore, in order to maintain high biodiversity in urban environments, it is crucial that we maintain more sub-natural areas within the city in which both adapters and avoiders can persist, in addition to the exploiters. Such decisions could benefit greatly from the inclusion of urban areas in future conservation and biogeographical studies.

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BIOSKETCHES

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APPENDIX 1a

A list of the urban species in Israel based on the literature (see Methods), their classification into urban exploiters and adapters, and the life-history traits examined. Legend for traits is given below.

Species	Latin name	Exploit/ adapt	Migrate	Sociality	Mating	Territoriality	Sex dimorphism	Seasonal dimorphism	Diet	Nest density
Feral pigeon	<i>Columba livia</i>	Exploit	S	F	M	N	Y	N	S,F	C
Palm (laughing) dove	<i>Streptopelia senegalensis</i>	Exploit	S	F	M	Y	Y	N	S,F	P/LC
House sparrow	<i>Passer domesticus</i>	Exploit	S	F	M	Y	Y	Y	S,F,I	LC/C
Hooded crow	<i>Corvus corone corvix</i>	Exploit	S	F	M	Y	N	N	O	P/LC
Common swift	<i>Apus apus</i>	Exploit	M	F	M	N	N	N	I	C
Spectacled bulbul	<i>Pycnonotus xanthopygos</i>	Adapt	S	P	M	Y	N	N	S,F,I	P
Palestine sunbird	<i>Nectarinia osea</i>	Adapt	S	S/P/SG	M	Y	Y	N	F,I	P
Great tit	<i>Parus major</i>	Adapt	S	S/SG	M	Y	S	VL	S,F,I	P
Red-rumped swallow	<i>Hirundo daurica</i>	Adapt	M	F	M	Y	N	N	I	LC
Barn swallow	<i>Hirundo rustica</i>	Adapt	S/M	F	M	N	S	VL	I	LC
Common house martin	<i>Riparia riparia</i>	Adapt	M	F	M	N	N	N	I	C
White wagtail	<i>Motacilla alba</i>	Adapt	M	S/P/F	M	Y	Y	Y	I	P
Common blackbird	<i>Turdus merula</i>	Adapt	S/M	S/P/SG	M	Y	Y	N	F,I	P
Eurasian jay	<i>Garrulus glandarius</i>	Adapt	S	S/P/SG	M	Y	N	VL	O	P
Lesser kestrel	<i>Falco naumanni</i>	Adapt	M	F	M	N	Y	N	I	C
Common kestrel	<i>Falco tinnunculus</i>	Adapt	S/M	P/SG	M	Y	Y	N	I,V	P/LC
Rose-ringed parakeet	<i>Psittacula krameri</i>	Adapt	S	F	M	Y	Y	N	S,F	P
Barn owl	<i>Tyto alba</i>	Adapt	S	S/P	M	N	Y	N	I,V	P
Eurasian hoopoe	<i>Upupa epops</i>	Adapt	S/M	S/P	M	Y	N	Y	F,I	P

Migrate: S – sedentary, M – migratory; sociality: S – solitary, P – pairs, SG – small groups, F – flocks; mating system: M – monogamous, P – polygamous; territoriality: Y – yes, N – no; sexual dimorphism: Y – yes, S – slight, N – none; seasonal dimorphism: Y – yes, S – slight, N – none; diet: S – seeds, I – invertebrates, N – nectar, F – fruit, V – vertebrates, H – herbs/plant material; nest density: P – pairs, LC – loose colonies, C – colonies.

Appendix 1b

Species	Latin name	Nest site	Nest construction	Nest cycles	Clutch size	Developmental mode	Incubation	Fledging	Brain volume	Body mass	Innovation rate
Feral pigeon	<i>Columba livia</i>	H/B	B	3	2	A	18	37	2.02	300	Low
Palm (laughing) dove	<i>Streptopelia senegalensis</i>	T/B	B	3	2	A	15	16	1.24	101	Low
House sparrow	<i>Passer domesticus</i>	H/B	M	2	6	A	14	15	1.00	23.5	Average
Hooded crow	<i>Corvus corone corvix</i>	C	B	1	4	A	21	30	8.51	536.5	High
Common swift	<i>Apus apus</i>	H	B	1	2.5	A	19	45	0.67	37.6	Average
Spectacled bulbul	<i>Pycnonotus xanthopygos</i>	T/B	F	2	3.5	A	14	14			Average

Appendix 1b *continued*

Species	Latin name	Nest site	Nest construction	Nest cycles	Clutch size	Developmental mode	Incubation	Fledging	Brain volume	Body mass	Innovation rate
Palestine sunbird	<i>Nectarinia osea</i>	T/B	F	2	3	A	12	13			Average
Great tit	<i>Parus major</i>	H	F	2	6	A	13	20	0.83	16	Average
Red-rumped swallow	<i>Hirundo daurica</i>	H/B	B	2	4	A	14	20			Average
Barn swallow	<i>Hirundo rustica</i>	B	B	2	4.5	A	14	21	0.55	18.5	Average
Common house martin	<i>Riparia riparia</i>	B	B	2	4	A	15	21	0.48	14.5	Average
White wagtail	<i>Motacilla alba</i>	H		2	5	A	12	14	0.6	24.4	Average
Common blackbird	<i>Turdus merula</i>	T	F	2	3	A	14	14	1.9	87.8	Average
Eurasian jay	<i>Garrulus glandarius</i>	H	B	1	4	A	17	20	4.05	170	High
Lesser kestrel	<i>Falco naumanni</i>	H		1	4	SA	28	27	2.71	151.5	High
Common kestrel	<i>Falco tinnunculus</i>	H/B/T		1	5	SA	28	30	3.87	214	High
Rose-ringed parakeet	<i>Psittacula krameri</i>	T	B	1	3.5	A	23	45	3.9	134.2	Average
Barn owl	<i>Tyto alba</i>	H/B		2	6	SA	30	60	6.51	523.5	
Eurasian hoopoe	<i>Upupa epops</i>	H/B	B	2	5.5	A	18	22	1.35	61.4	

Nest site: H – hole, B – building, T – trees and shrubs, G – ground, CAT – cattails; nest construction: M – male, F – female, B – both; developmental mode: A – altricial, SA – semi-altricial, P – precocial.