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Changes in the home range sizes of terrestrial vertebrates in response to urban disturbance: a meta-analysis

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Abstract

The unprecedented growth rate in human population and the increasing movement of people to urban areas is causing a rapid increase in urbanisation globally. Urban environments may restrict or affect the behaviour of many animal species. Importantly, urban populations may change their spatial movement, particularly decreasing their home ranges in response to habitat fragmentation, the presence of landscape barriers and the availability and density of resources. Several species-specific studies suggest that urban animals decrease their home ranges compared with their non-urban counterparts; however, it remained unclear whether this pattern is widespread across taxa or is instead restricted to specific taxonomic groups. Consequently, we conducted a meta-analysis, collecting 41 sets of data comparing home ranges in both natural and urban environments in 32 species of reptiles, birds and mammals. We calculated effect sizes as the difference in animal home range sizes between natural and urban environments. We found that the home ranges were smaller in urban environments compared with natural environments (mean effect size = −0.844), and we observed a similar result when considering birds and mammals separately. We also found that home range sizes were not significantly affected when disturbance in urban areas was minimal, which suggests that many species may be able to tolerate low levels of disturbance without changing their movement patterns. Our study thus indicates that increasing levels of urbanisation restrict the spatial movement of species across taxa; this information is relevant for ecological studies of further urban species as well as for the development of management strategies for urban populations.

Key words: urban disturbance, habitat fragmentation, home range, terrestrial vertebrates, urban environments, urbanisation

Introduction

Natural habitats are rapidly being converted into urban and highly anthropogenic landscapes to accommodate and sustain the increasing global human population (United Nations Population Division 2018). Urbanisation is changing the environment available to animals by increasing temperature, noise and air pollution, the number of barriers preventing wildlife movement and the percentage of impervious surfaces (Pickett et al. 2001; Johnson and Munshi-South 2017). Urbanisation also impacts species through multiple changes in food resource availability, habitat composition, intra- and inter-specific competition and predation rates (Luck and Smallbone 2010; Sol, Lapiedra, and González-Lagos 2013; Boggie and Mannan 2014). As a response to these ecological changes, urban animals can adjust their behaviour (e.g. feeding, activity patterns, responses

to humans and social behaviour) to survive in urban environments (Bateman and Fleming 2012; Lowry, Lill, and Wong 2013; Sol, Lapiedra, and González-Lagos 2013; Bateman and Fleming 2014; Johnson and Munshi-South 2017).

A consequence of urbanisation that is particularly challenging for many species is the loss and fragmentation of their natural habitat (Červinka et al. 2014; Donihue and Lambert 2015). Suitable habitat fragments scattered and connected throughout an urban environment may be key for the survival of a species (Bateman and Fleming 2012). Habitat changes and the fragmented distribution of resources across urban landscapes may favour habitat generalists (Clergeau et al. 2006; Concepción et al. 2015) and may also result in animals changing their movement patterns and space use, especially by altering the size of their home ranges (Greenspan, Nielsen, and Cassel 2018).

The home range of a species is the area individuals use to rear their young, find resources and secure mates (Börger et al. 2006; Powell and Mitchell 2012; Walton et al. 2017). Home range size varies depending on many factors, such as energy requirements, habitat productivity, population density, predation rate, social structure, body size, sex and seasonality (Burt 1943; Powell and Mitchell 2012; Walton et al. 2017). A home range is determined not only by environmental factors but also by how individuals within a species perceive the resources available within a specific environment (Börger et al. 2006; Powell and Mitchell 2012).

Some studies have suggested that home range sizes decrease in urban environments compared with natural environments. For example, a meta-analysis on eight carnivore species showed that home ranges decreased along rural–urban gradients (Šálek, Drahníková, and Tkadlec 2014). There are several possible explanations for such a decrease in home ranges in urban environments. First, habitat fragmentation may physically limit the expansion of home ranges, with roads, buildings, walls and fences preventing normal movement and habitat connectivity. Species such as bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) would have larger home ranges in unfragmented landscapes but may be forced to survive in smaller habitat fragments when suitable corridors are not available, as roads and buildings may create a hostile urban matrix that is hard for them to travel across (Tigas, Van Vuren, and Sauvajot 2002). Second, higher population densities may prevent the expansion of home ranges into areas already occupied by conspecifics (Červinka et al. 2014; Magle et al. 2014; Mitsuhashi et al. 2018; Tucker et al. 2018). Higher population densities also increase mating opportunities within a smaller area, making large home ranges to access more possible mates unnecessary (Riley et al. 2003). Third, an increase in local resources such as shelter and food in urban environments may also lead to animals restricting their movement because they do not need to move over large areas to exploit those resources (Šálek, Drahníková, and Tkadlec 2014; Mitsuhashi et al. 2018). Prey species may be more abundant in urban habitats because of higher availability of anthropogenic food (Fischer et al. 2012). In turn, predator species in urban environments may benefit from high densities of prey such as small mammals and insects and their diet can also be supplemented with anthropogenic food such as refuse from rubbish bins, crops, pet food, garden fruit and vegetables, road kill and pets (Bateman and Fleming 2012; Červinka et al. 2014; Šálek, Drahníková, and Tkadlec 2014).

However, it was still unclear whether a decrease in home range size in urban populations is a general pattern across taxonomic groups, and whether such a pattern emerges even in response to low levels of urbanisation. Here, we conducted a meta-analysis to determine the impact of urbanisation on the home ranges of vertebrate species. We compiled studies making a direct comparison between the home ranges of any terrestrial vertebrate in both natural and urban environments. We addressed two main questions. First, we determined if across taxa the home ranges of urban populations decrease compared with non-urban populations. Second, we considered different levels of disturbance in urban environments and their effects on home range sizes. We predicted that only high levels of disturbance, but not minimal levels of disturbance, result in significant changes in home range size. Addressing these questions is important to understand how increasing rates of urbanisation may affect the distribution and colonisation potential of species across cities worldwide, and to decide how better implement management strategies involving species in urban environments given their spatial flexibility and requirements.

Methods

Literature search and data handling

We conducted a series of literature searches in Web of Science between 11 October and 13 November 2018 using a combination of two keywords. The first keyword was related to urbanisation and included one of the following terms: urban*, city, suburban*, metropolitan, 'inner-city', town, citified, municipal*, metropolis, civilisation, 'megacity' or village. The second keyword was related to home range and included one of the following terms: 'territory size', 'habitat range', 'territory range', 'animal's territory', 'habitat size' or 'home range'. We chose any keywords that we thought could result in publications studying spatial distribution of animals in relation to urbanisation, i.e. we did not select a restricted set of keywords from a larger pool of options. Search words with an asterisk allowed for different forms of a word to appear in the search results (e.g. the term urban* searched publications containing the words urban, urbanised, urbanized, urbanisation, urbanization, etc.). Quotation marks limited results to cases in which the words in question appeared together. These combined literature searches resulted in 654 publications. Of these, 331 publications included some measurement of home range or territory size. We only selected publications that reported such measurements in both natural and urban environments, i.e. studies involving a comparison of different environments along a natural-urban gradient. We use the term 'natural' environment to refer to the sites selected in each study as a comparison to urban sites. We considered studies in any continent, i.e. we did not use any type of geographic restriction.

We discarded any studies in which any sample size was 1 (sample sizes for the selected studies can be seen in Table 1). This process led to a dataset with 39 natural-urban comparisons. We then searched in Web of Science (25 June 2019) for all the studies that had cited the studies present in our dataset. After following a filtering process as described above, we added 2 more comparisons, for a total of 41 comparisons, which included 32 species (3 reptiles, 10 birds and 19 mammals; Table 1). We did not find any relevant studies on amphibians.

For each natural-urban comparison, we compiled the mean home range size, standard deviation (SD) and sample size for both the natural environment and the urban environment

Table 1: Species included in the meta−analyses, summary of the original data (means±SD and sample sizes for home range sizes in natural and urban areas) and calculated Hedge's d and variance

Species	Common name	Natural HR (mean±SD; n)	Urban HR (mean±SD; n)	Hedge's d	Variance d	Measure; method	Reference
Accipiter cooperii	Cooper's hawk	609 ± 323.11; 4	481 ± 153.79; 4	−0.439	0.512	ha; RT	Chiang et al. (2012)
Accipiter cooperii	Cooper's hawk	14.2 ± 1.27; 2	3.9 ± 3.2; 4	−2.890	1.446	km^2; RT	Roth, Vetter, and Lima (2008)
Alces alces	Moose	106 ± 83.33; 49	55 ± 14; 25	−0.737	0.064	km^2, GPS, RT	Wilson et al. (2015)
Anas fulvigula	Mottled duck	551.05 ± 749.22; 104	5.06 ± 353; 89	−0.906	0.023	km^2; RT	Varner, Hepp, and Bielefeld (2014)
Buteo regalis	Ferruginous hawk	4.71 ± 6.65; 25	2.3 ± 1.80; 13	−0.427	0.119	km^2; RT	Plumpton and Andersen (1998)
Canis aureus	Golden jackal	21.2 ± 9.3; 8	6.6 ± 4.5; 8	−1.889	0.362	km^2; RT	Rotem et al. (2011)
Canis latrans	Coyote	16.5 ± 1.39; 3	15.4 ± 15.43; 6	−0.075	0.500	km^2; RT	Bounds and Shaw (1997)
Corvus brachyrhynchos	American crow	8569.85 ± 9568.32; 6	1452.7 ± 12729; 36	−0.564	0.198	ha; RT	Marzluff and Neatherlin (2006)
Corvus corax	Common raven	2743.08 ± 3512.4; 9	492.14 ± 1019.38; 21	−1.060	0.177	ha; RT	Marzluff and Neatherlin (2006)
Cyanocitta stelleri	Steller's jay	65.45 ± 75.11; 15	46.83 ± 66.45; 10	−0.251	0.168	ha; RT	Marzluff and Neatherlin (2006)
Cyanocitta stelleri	Steller's jay	15 ± 6.33; 10	16.4 ± 11.63; 20	0.133	0.150	ha; RT	Goldenberg, George, and Black (2016)
Felis catus	Domestic cat	0.87 ± 0.86; 9	0.13 ± 0.23; 7	−1.043	0.288	ha; RT	Lilith, Calver, and Garkaklis (2008)
Felis catus	Domestic cat	61 ± 61.29; 13	7.44 ± 15; 25	−1.400	0.143	ha; GPS	Metsers, Seddon, and van Heezik (2010)
Heloderma suspectum	Gila monster	21.03 ± 5.87; 9	15.96 ± 12.98; 17	−0.442	0.174	ha; RT	Kwiatkowski et al. (2008)
Herpestes javanicus	Small Indian mongoose	11.44 ± 7.22; 7	8.31 ± 8.84; 7	−0.363	0.290	ha; RT	Quinn and Whisson (2005)
Lampropeltis californiae	California kingsnake	6.31 ± 8.43; 9	4.79 ± 4.42; 9	−0.215	0.224	ha; RT	Anguiano and Diffendorfer (2015)
Lynx rufus	Bobcat	831.86 ± 834.07; 11	323.09 ± 278.12; 8	−0.732	0.230	ha; RT	Riley (2006)
Macropus fuliginosus	Western grey kangaroo	41.8 ± 23.95; 14	60.9 ± 52.66; 6	0.531	0.245	ha; RT	Chachelle et al. (2016)
Masticophis flagellum	Coachwhip	136.4 ± 90.22; 6	22.44 ± 15.72; 18	−2.436	0.346	ha; RT	Mitrovich, Diffendorfer, and Fisher (2009)
Meles meles	Eurasian badger	305 ± 110.4; 15	168 ± 101.5; 19	−1.268	0.143	ha; RT	Kauhala and Auttila (2010)
Meles meles	Eurasian badger	576.74 ± 297.88; 19	134 ± 53; 6	−1.618	0.272	ha; RT	Kauhala and Holmala (2011)
Mungos mungo	Banded mongoose	162.5 ± 44.55; 2	46 ± 45.19; 8	−2.332	0.897	ha; GPS, RT	Laver and Alexander (2018)
Nyctereutes procyonoides	Raccoon dog	99 ± 39.7; 17	104 ± 30.1; 19	0.140	0.112	ha; RT	Kauhala and Auttila (2010)
Nyctereutes procyonoides	Raccoon dog	207.54 ± 127.32; 26	130 ± 46.3; 16	−0.728	0.107	ha; RT	Kauhala, Schregel, and Auttila (2010)
Nyctereutes procyonoides viverrinus	Raccoon dog	128 ± 94.19; 7	92.6 ± 53.4; 6	−0.420	0.316	ha; RT	Saeki, Johnson, and Macdonald (2007)
Odocoileus virginianus	White-tailed deer	67.5 ± 35.92; 7	34 ± 9.9; 9	−1.283	0.305	ha; RT	Kilpatrick, Spohr, and Lima (2001)
Passer domesticus	House sparrow	0.96 ± 0.69; 15	0.51 ± 0.48; 16	−0.743	0.138	ha; RT	Vangestel et al. (2010)
Petaurus norfolcensis	Squirrel glider	7.07 ± 1.36; 10	3.4 ± 0.82; 10	−3.128	0.445	ha; RT	Brearley et al. (2011)
Procyon lotor	Raccoon	18.27 ± 22.59; 5	1.91 ± 1.48; 5	−0.923	0.443	km^2; RT	Bartoszewicz et al. (2008)
Procyon lotor	Raccoon	226.64 ± 104.91; 33	127.91 ± 91.12; 46	−1.007	0.058	ha; RT	Bozek, Prange, and Gehrt (2007)
Procyon lotor	Raccoon	139.85 ± 79.61; 18	38.33 ± 44.46; 18	−1.540	0.144	ha; RT	Prange, Gehrt, and Wiggers (2004)
Pyrrhocorax graculus	Alpine chough	154.2 ± 21.87; 17	41.92 ± 26.4; 17	−4.523	0.418	km^2; RT	Rolando, Laiolo, and Carisio (2003)
Sciurus niger	Fox squirrel	139 ± 216.6; 45	53 ± 39.12; 60	−0.590	0.041	ha; RT	McCleery and Parker (2011)
Strix aluco	Tawny owl	22 ± 12.6; 17	17.6 ± 12.1; 22	−0.350	0.106	ha; NA	Galeotti (1994)
Sus scrofa	Wild boar	2.2 ± 0.94; 29	1 ± 0.6; 5	−1.295	0.259	km^2; RT	Podgórski et al. (2013)
Tyto furcata	Barn owl	1.87 ± 0.64; 3	14.75 ± 12.49; 4	1.118	0.673	km^2; RT	Hindmarch et al. (2017)
Urocyon cinereoargenteus	Gray fox	5.49 ± 1.77; 6	3.84 ± 1.46; 6	−0.938	0.370	km^2; RT	Harrison (1997)
Urocyon cinereoargenteus	Gray fox	63.75 ± 16.79; 12	71.76 ± 46.81; 16	0.209	0.147	ha; RT	Riley (2006)
Urocyon littoralis clementae	Island fox	0.82 ± 0.34; 18	0.72 ± 0.4; 25	−0.261	0.096	km^2; RT	Gould and Andelt (2013)
Ursus americanus	Black bear	376.78 ± 449.97; 17	53.24 ± 35.76; 24	−1.096	0.115	km^2; RT	Beckman and Berger (2003)
Vulpes vulpes	Red fox	927 ± 525.1; 16	431.19 ± 594.73; 19	−0.859	0.126	ha; RT	Gosselink et al. (2003)

HR, home range; RT, radio transmitter; NA, not available.

(Table 1). In the few cases in which more than two values along an environmental gradient were reported [e.g. values for rural, suburban and urban areas in Prange, Gehrt, and Wiggers (2004)], we selected the two most extreme values along that gradient (i.e. rural vs. urban in the previous example), as this provided a better natural vs. urban comparison.

In the majority of studies, data were obtained using radiotelemetry (Table 1). Home range sizes were calculated using different methods, the main ones being minimum convex polygon (MCP) and fixed kernel density (FKD). The MCP method involves delineating the smallest possible convex polygon around the available data, whereas the FKD methods are statistical approaches to estimate home ranges (Kie et al. 2010). The MCP method tends to overestimate the real home range; FKD approaches can provide more realistic estimates, but assumptions are made during the estimations that can introduce biases if incorrectly applied (Kie et al. 2010). The MCP method has been a more common method, although alternative methods are being used more frequently in recent years (Kie et al. 2010). Some publications reported these calculations at different percentages, e.g. 80% FKD, 90% FKD, 95% FKD, 95% MCP or 100% MCP, although home ranges are most commonly estimated at a 95% utilisation distance. For consistency purposes, when several methods of home range estimation were reported, we chose 95% MCP, as this is the method used in the majority of studies that we considered.

When values for males and females were reported separately, we pooled both values, calculating weighted means and SDs. We did this to increase consistency in our dataset, as in several studies values were reported without considering sex. In one case in which the available information did not allow us to calculate weighted means and SDs, we used results from males (McCleery and Parker 2011). We estimated the SD values when other measures of dispersion were reported. For a 95% confidence interval, we divided the length of the confidence interval by 3.92 and then multiplied by the square root of the sample size. When only standard errors of the mean were reported, we multiplied that value by the square root of the sample size to obtain the SD. When median and interquartile range (IQR) were reported, we used the median value as the mean and divided the IQR value by 1.35 to estimate the SD. When necessary, we extracted data from figures using WebPlotDigitizer 4.2 (apps.automeris.io/wpd/).

Statistical analyses

We conducted meta-analyses to determine whether home range sizes differ between natural and urban environments. A meta-analysis is a quantitative approach that synthesises a series of independent studies addressing a similar question (Wallace et al. 2017). Briefly, an effect size is calculated for each individual study. In this case, the effect size would be a measure of the difference in home range size between natural and urban environments. A meta-analysis combines all those effect sizes into an estimate of the overall strength of the effect and determines whether the overall effect size is statistically significant from zero.

We implemented all meta-analyses using OpenMEE (Open Meta-analyst for Ecology and Evolution; 2015-11-15 build date; cebm.brown.edu/openmee) (Wallace et al. 2017). For each natural-urban comparison we calculated an effect size (Hedge's *d*) for the difference between the natural environment and the urban environment. Hedges's *d* is calculated by dividing the difference in means by the pooled and weighted SD, and its use is recommended for studies with small sample sizes. We calculated each Hedges' *d* and variance in OpenMEE using the mean, SD and sample size for the two sets of data (i.e. natural and urban environments; Table 1). Positive effect sizes indicated that home ranges were larger in urban environments than in natural environments. Negative effect sizes indicated the opposite. As a rough guide, effect sizes of 0.2, 0.5 and 0.8 (with either a positive or negative sign) are normally interpreted as being small, medium and large, respectively (Cohen 1988).

First, we conducted a subgroup meta-analysis, considering the overall effect across all species, as well as considering reptiles, birds and mammals separately (i.e. running separate meta-analyses for each taxonomic group). We used a DerSimonian–Laird random-effects method (DerSimonian and Laird 1986). We also conducted a meta-analysis in which we divided the natural-urban comparisons depending on the level of contrast between the two types of environments. We considered three levels of contrast (low, intermediate and high). The low contrast included studies in which the level of urban disturbance was minimal, e.g. lack of vs. scattered residential buildings in a natural reserve. The intermediate contrast included studies in which the disturbed area contained low levels of urbanisation, e.g. villages within a natural matrix, or suburban areas around small towns. The high contrast included highly urbanised areas, e.g. suburban areas around large cities, or city centres. In this case, we also implemented a subgroup meta-analysis within OpenMEE, with a DerSimonian–Laird random-effects method.

To determine the possible existence of publication bias we used the fail-safe N approach. In this case the fail-safe N estimated the number of additional studies that would be required to find no differences in home range size between natural and urban environments (Orwin 1983). A low fail-safe N would indicate that studies that went unpublished because they found no statistical differences between natural and urban areas could affect the overall results of our study if they had been part of our dataset.

Results

In the majority of comparisons, home ranges were smaller in the urban environment than in the natural environment (Table 1). Out of the 41 comparisons under consideration, 36 had negative effect sizes and only 5 had positive effect sizes. Moreover, none of the positive effect sizes had a 95% confidence interval not including zero, indicating that the difference in home range between natural and urban environments in those four cases was not significant (Fig. 1).

The overall effect size across the 41 comparisons was -0.844, which was highly significant (95% CI: -1.07 to -0.62; $P < 0.001$). This value indicates that home ranges across taxa are much smaller in urban than in natural environments. Similar effect sizes were found for reptiles (-0.977), birds (-0.787) and mammals (-0.863), although these effect sizes were significantly different from zero only in the case of birds (-1.3 to -0.28 CI; $P = 0.002$) and mammals (-1.11 to -0.61 CI; $P < 0.001$), but not in the case of reptiles (-2.21 to 0.26; $P = 0.12$), given that only three reptilian natural-urban comparisons were available. Heterogeneity (the level of variation between studies due to true among-study differences rather than chance) was high when including all comparisons ($I^2 = 67.74\%$, $P < 0.0005$) or when considering reptiles ($I^2 = 80.01\%$, $P = 0.007$), birds ($I^2 = 79.4\%$, $P < 0.0005$) or mammals ($I^2 = 58.61\%$, $P < 0.0005$) separately.
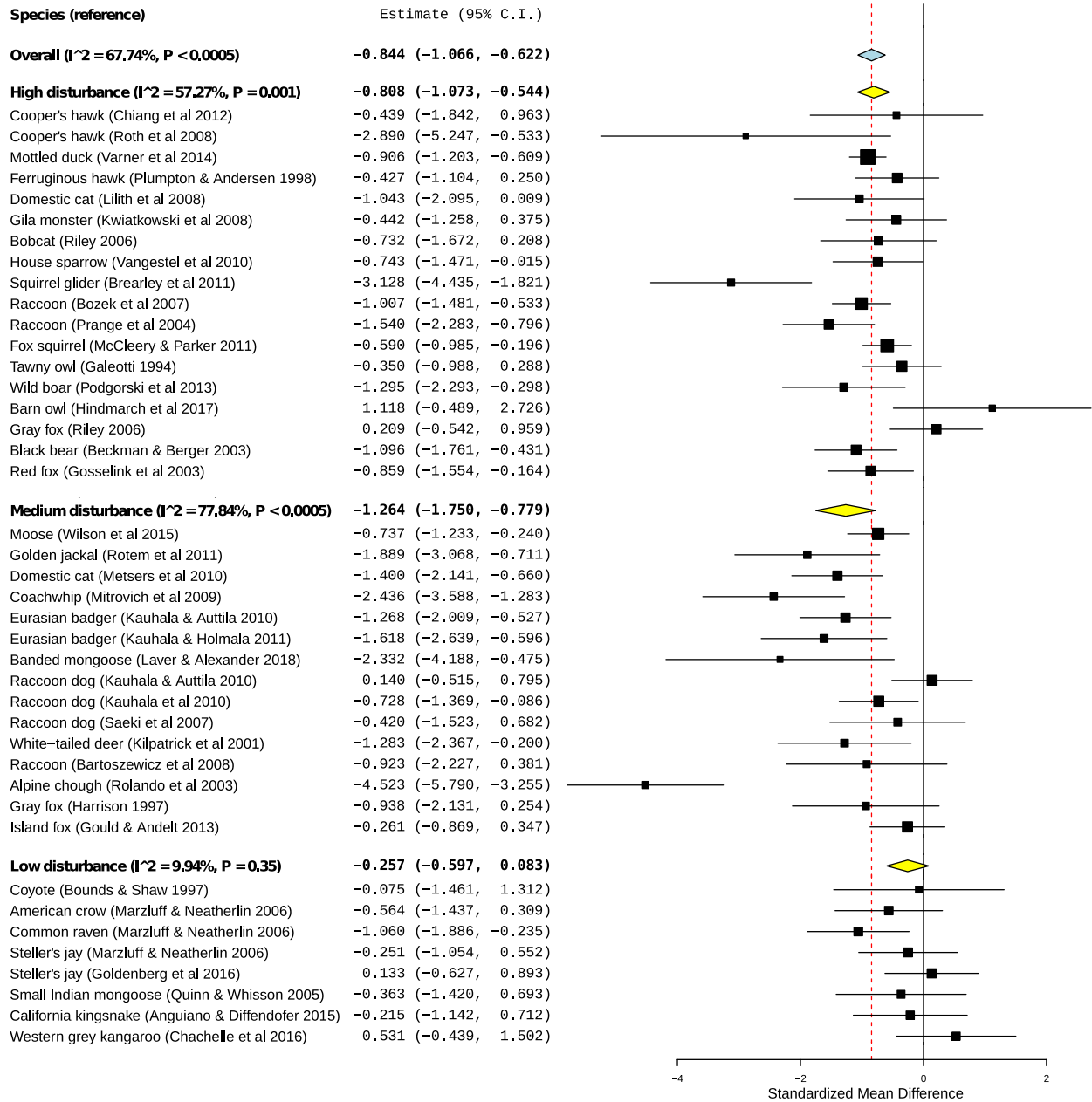
Figure 1: Forest plot of the effect sizes (standardised mean difference between natural and urban home range sizes) and their 95% confidence intervals. Negative effect sizes indicate that home ranges were smaller in urban areas than in natural areas. The horizontal lines represent the 95% confidence intervals, and the areas of the black squares reflect each study weight (smaller symbols indicate higher variances and smaller weights). The overall effect size is indicated by the top diamond (the centre of the diamond represents the overall effect size and the tips the 95% confidence interval). The perpendicular dotted red line also represents the overall effect size. The yellow diamonds represent the effect size and 95% confidence intervals for the three types of disturbance (high, medium and low). If any confidence interval includes 0 (marked by the solid vertical line) the difference in the effect between natural and urban areas is not statistically significant.

When we grouped comparisons by the level of disturbance in the urban environment, we found negative and significant effects (i.e. smaller home ranges in the urban environment) when the level of disturbance was high (as in highly urbanised areas; effect size: -0.808; -1.07 to -0.54 CI; $P < 0.001$) or medium (effect size: -1.264; -1.75 to -0.78; $P < 0.001$). However, at low levels of disturbance the effect size (-0.257) was not significantly different from zero (-0.6 to 0.08 CI; $P = 0.14$). Heterogeneity was low in studies with

low disturbance ($I^2 = 9.94\%$, $P = 0.35$), but high and statistically significant in studies with medium disturbance ($I^2 = 77.84\%$, $P < 0.0005$) or high disturbance ($I^2 = 57.27\%$, $P = 0.001$).

The fail-safe N (the estimated number of additional studies that would be required to find no differences in home range size between natural and urban environments) was 2483. Such a high value indicates that publication bias is unlikely to be a concern in this case.

Discussion

We found that across taxa, home ranges are significantly smaller in urban environments than in natural environments. We also found that such pattern only emerges at medium and high levels of urban disturbance, but not at low levels of urban disturbance.

We detected a similar decrease in home range sizes in urban environments when we considered separately birds and mammals. This is an important result, which highlights that change in home ranges driven by urbanisation may be consistent across taxonomic groups. In the case of reptiles, the low number of studies that we considered prevented us from discerning a clear pattern. In fact, urbanisation did not lead to changes in home range size in two of the three species in our analyses, possibly for different reasons: the California kingsnake (*Lampropeltis californiae*) has naturally small home ranges, which may not be able to decrease further in urban environments; whereas the Gila monster (*Heloderma suspectum*) was studied in areas with low levels of urbanisation (Kwiatkowski et al. 2008; Anguiano and Diffendorfer 2015).

There are several explanations for the reduction that we found in the home ranges of animals living in urban environments. For example, species living in urban environments may have smaller home ranges when they have access to a reliable and abundant food supply nearby, not needing to travel far to access it (Bino et al. 2010; Reher et al. 2016; Mitsuhashi et al. 2018). A higher availability of resources other than food (e.g. shelters) may similarly lead to smaller home ranges in urban landscapes (Rutz 2006; Šálek, Drahníková, and Tkadlec 2014). The abundance of conspecific competitors in an area may also affect a species home range size (Galeotti 1994; Boggie and Mannan 2014). Species often occur in much higher densities in urban areas than in rural environments (Walton et al. 2017). For example, species such as red fox (*Vulpes vulpes*), skunk (*Mephitis mephitis*) and raccoon (*Procyon lotor*) are present at their highest densities in highly urbanised environments (Riley et al. 2003). In species in which movement across the home ranges of other conspecifics is difficult or dangerous (e.g. due to territorial aggression), higher population densities will lead to reduced home ranges, especially when the available urban space is a limited resource.

The level of urban disturbance across the studies that we considered was highly variable, from campground areas in protected parks to the centre of large cities. We found that the size of home ranges was not affected when the level of urban disturbance was low. However, when the level of disturbance increased, home ranges became significantly smaller. This type of result indicates that many native species may be relatively resilient to low levels of urban disturbance, and thus that areas that are minimally disturbed may contain appropriate habitats for the conservation of targeted species.

Even though we detected a clear pattern in which urbanisation leads to a reduction of home range size across taxa, a major limitation of this study is the large number of confounding variables that we were not able to investigate due to the relatively low number of available studies. In fact, the heterogeneity values that we found, which measures the variation due to amongst-study differences, were very high when including all comparisons, as well as when considering reptiles, birds or mammals separately. This is not surprising, given the large differences among studies, for example concerning the type of urban disturbance, the method for estimating home ranges or the area sizes regularly used by different species. In relation to levels of disturbance, heterogeneity was very low in studies with low disturbance, but much higher in studies with medium disturbance and high disturbance. As there are many different types of urban disturbance, higher levels of disturbance are likely to increase variation across studies. This implies that one should be careful extrapolating results from one species in one city to other species and cities, or when different types of disturbance are considered.

Similarly, we did not assess seasonal variation in urban home ranges, as this type of data was scant. We were also unable to investigate how the location of the home range of an animal may change across urban gradients at different times of the year. In studies comparing animals in urban vs. natural areas, there may be a tendency to assume that there are distinct urban and natural populations with differentiated behavioural strategies. However, in some species animals may transition between those environments throughout the year. For example, as resources become restricted during the winter in natural areas some animals may move into urban areas to meet their resource requirements (Luck and Smallbone 2010). However, this may not be the case in highly territorial species or when movement is restricted by physical barriers. How individual animals may change their home range sizes and spatial usage as they seasonally transition between natural and urban areas deserves further investigation.

Even though we found a general pattern for home ranges to be reduced in urban environments, there are exceptions to this pattern. For example, a positive association between the degree of urbanisation and home range size has been reported for coyotes (Riley et al. 2003) and barn owls (*Tyto furcata*) (Hindmarch et al. 2017). Such predators may require larger home ranges in urban areas, as they need to incorporate many habitat fragments in their territories in order to obtain enough prey (Hindmarch et al. 2017).

In conclusion, many species' home ranges decrease substantially in size in urban environments. This can be due to species adapting to urban life and being able to exploit a high variety of resources, or because they have no choice as habitat loss, fragmentation and landscape barriers limit their space use (Bino et al. 2010). In any case, the spatial changes that we found across taxa highlight the importance of continuous studies on urban ecology, as knowledge about natural populations may not be extrapolated to our understanding of urban populations. Such an understanding about urban populations can in turn better inform urban design and improved strategies for human–animal coexistence. For example, knowing that urban animals from many species can survive and even thrive in relatively small spaces can change the notion that only extensive green urban spaces can sustain viable biodiversity, highlighting the importance of smaller urban spaces if properly managed. As urban areas are rapidly expanding into natural areas more research needs to be conducted to further understand and quantify the impacts of urbanisation at all levels of an ecosystem if we want to maximise urban biodiversity and the long-term persistence of urban populations.

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