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Review Article

A meta-analysis indicates reduced predation pressure with increasing urbanization

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ABSTRACT

Urbanization is one of the most important global trends which causes habitat reduction and alteration which are, in turn, the main reasons for the reduced structural and functional diversity in urbanized environments. Predation is one of the most important ecological functions because of its community-structuring effects. According to previous studies effects of urbanization on predation rates appear inconsistent. Predator species are vulnerable to habitat alteration and loss caused by urbanization, therefore, we hypothesised that predation rate would decrease along the rural-urban gradient. To clarify the impact of urbanization on predation, we performed a meta-analysis on predation rates in rural vs. urban areas using published data of 25 studies. Predation rates on taxa other than birds were underrepresented, preventing an overall evaluation. Reported predation rates on birds were significantly higher in rural than in urban habitats.

1. Introduction

Urbanization is one of the most important processes shaping our environment (McKinney, 2006, 2008), with fewer people living today in rural than urban areas globally (United Nations & Department of Economic and Social Affairs, 2014). In particular, urbanization impacts biodiversity in a variety of ways. For instance, urbanization results in new assemblages of species (Stracey & Robinson, 2012). The outcome of urbanization includes decreased survival rates of species due to disease, starvation, novel toxins, collisions with structures or vehicles, electrocution, and predation (Newton, 1998). Furthermore, urbanization can impact body size (Weller & Ganzhorn, 2004), body size distribution (Magura, Tóthmérész, & Lövei, 2006), fluctuating asymmetry (Elek, Lövei, & Bátki, 2014), reproduction rates (Seress et al., 2012), and migratory behavior (Partecke & Gwinner, 2007). Urbanization does not necessarily result in losses in species richness or taxonomic diversity (Magura, Lövei, & Tóthmérész, 2010), but habitat specialists often disappear from modified areas (Devictor, Julliard, Couvet, Lee, & Jiguet, 2007; Liker, Papp, Bókony, & Lendvai, 2008; Lövei, Magura, Tóthmérész, & Ködöböcz, 2006), functional diversity can decrease (Sacco et al., 2015) and evolutionary distinctness is lost (La Sorte et al., 2018). Finally, urbanization can change biogeochemical cycles (Grimm, Hale, Cook, & Iwaniec, 2015) and trophic interactions (pollination: Harrison & Winfree, 2015; parasitism: Fenoglio, Videla, Salvo, & Valladares, 2013; predation: Ferrante, Lo Cacciato, & Lövei, 2014).

Predation is one of the most important ecological processes because of its community-structuring effects but urbanization may strongly impact predator-prey dynamics (Shochat, Warren, Faeth, McIntyre, & Hope, 2006). The predator communities of natural and semi-natural habitats differ from those in urban habitats (Haskell, Knupp, & Schneider, 2001). For example many predators avoid urban areas, at least during daytime (Tigas, Van Vuren, & Sauvajot, 2002). Synanthropic predators can become frequent in urban environments (Haskell et al., 2001). Predator populations (Scanlon & Petit, 2008) and predation rates (Gering & Blair, 1999) can also increase markedly in urban areas due to such factors as increased lighting (Gaston, Bennie, Davies, & Hopkins, 2013) and bird feeding (Clergeau, Savard, Mennechez, & Falardeau, 1998) which attracts prey. Finally, just the perceived risk of predation can lead to alterations in behaviour that affect demographic factors and species interactions (Avilés & Bednekoff, 2007; Tholt et al., 2018). Overall, it is difficult to predict impacts of urbanization on predation, and indeed different studies report predation rates in rural landscapes that are lower (Jokimäki & Huhta, 2000; Thorington & Bowman, 2003), higher than (Gering & Blair, 1999) or similar to (Haskell et al., 2001) urban areas.

Predation risk also has a component of fear of being killed by a predator and this modifies the prey's foraging behaviour (Laundre, Hernandez, & Ripple, 2010). Leafhoppers feed less frequently and are

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more cautious when spiders are present (Beleznai et al., 2015). In urban habitats, wild boar (*Sus scrofa*) have higher tolerance against disturbance, demonstrated as shorter flight distance and increased re-use of areas around traps (Stillfried et al., 2017). Urban light pollution influences predation risk, but it does not affect the foraging behaviour of the white-footed mice (*Peromyscus leucopus*) (Persons & Eason, 2017) and Dalmatian wall lizard's (*Podarcis melisellensis*) behaviour does not differ between rural and urban habitats, either (De Meester et al., 2018).

Given the variety of ways that urbanization leads to different opportunities for predators, there have been several hypotheses that sought to provide explanations. Two of the main hypotheses related to urban predators are the predator relaxation or safe habitat hypothesis (Noske, 1998) and the predation proliferation hypothesis (Sorace, 2002). The predator relaxation/safe habitat hypothesis predicts that there is less mortality in urban areas due a reduced number of predators (Gering & Blair, 1999). This lower number of predators also reduces the need for vigilance, allowing more time for alternative activities, such as looking for better quality food, better progeny care, thereby also bringing indirect benefits to prey species (Valcarcel & Fernández-Juricic, 2009). In the case of birds, the lack of major nest predators in urban habitats, prey switching of urban predators, or efficient nest defence against nest predators are reasons for predation relaxation (Stracey, 2011). Notably, Gray's increasing disturbance hypothesis (Gray, 1989) predicts species loss along the rural-urban gradient and some of the lost species will be predators. Hence, the increasing disturbance hypothesis can result in a similar outcome of decreased predation rates along the rural-to-urban gradient as the predator relaxation hypothesis.

The second main hypothesis is the predation proliferation hypothesis, which predicts that certain predators can adapt to urban environments and increase their densities (Sorace, 2002), leading to greater predation pressure in urban than rural areas (Fischer, Cleeton, Lyons, & Miller, 2012). Increased predation in urban areas can be from the opportunistic predators whose main feeding is by scavenging (e.g., the European fox (*Vulpes vulpes*); Contesse, Hegglin, Gloor, Bontadina, & Deplazes, 2004) and are thus decoupled from the fluctuations in prey density. They can keep high densities and exert a continuously high predation pressure on their prey. Because both the predation relaxation and predation proliferation hypotheses have support in the literature, our objectives were to test whether there are general patterns of predation change in rural versus urban landscapes and if so, whether they support one or the other of the two main hypotheses.

To determine whether the literature supports predation relaxation or the predator proliferation hypothesis, we tested whether general patterns of predation differ in rural versus urban landscapes by performing a meta-analysis. Our review supported the predation relaxation hypothesis, but not the predator proliferation one: predation rates on birds were significantly higher in rural than in urban habitats.

2. Material and methods

2.1. Literature search and compilation of the relevant dataset

We used the PRISMA guidelines through the study selection process (Moher, Liberati, Tetzlaff, Altman, & PRISMA Group, 2009). We searched for information on all the databases available under the Web of Knowledge umbrella, that now combines several large databases, including the Web of Science, BIOSIS and CABI. We used the search string: TOPIC: (urbanis*) OR TOPIC: (urbaniz*) (producing 32,158 records) after which we refined the results using the REFINE (predat*) AND (rural) command. This refining process identified 139 publications (details see in Fig. S1). Subsequently, we checked the reference list of the 139 papers identified, which added 121 records, resulting in a total of 246 papers for evaluation after the duplicates were removed. We examined all these papers and included those which 1) were conducted in unequivocally defined rural as well as urban habitats and 2) reported means of predation rates.

We found 25 studies meeting our criteria. Multi-year research was considered as one dataset (16 papers). One paper could be included multiple times, if it had information on several species, nest placements, prey age group or study areas. We had six studies that provided such multiple accounts (Gering & Blair, 1999; Jokimäki et al., 2005; Matthews, Dickman, & Major, 1999; Rodewald, Kearns, & Shustack, 2011; Stracey & Robinson, 2012; Tella, Hiraldo, Donázar-Sancho, & Negro, 1996).

In all cases, we accepted the authors' classification of urbanization degree. In most studies, rural and urban habitats were close to each other, but in Tella et al., (1996) this distance was about 750 km. We included data from Tella et al.'s (1996) paper, because the authors studied the same species in the same climatic zone. Several (but not all) papers contained data on predation in suburban habitats, which were excluded, in order to have a maximum contrast between the two ends of the urbanization gradient. One study (Roth, Lima, & Vetter, 2005) found no predation in either rural or urban sites and was excluded.

From 25 studies that passed the inclusion criteria, we extracted data on study location, duration, date, prey type (natural or artificial), prey age group (egg, larva, nestling, juvenile, adult), predators identified (to the highest resolution given) and identification method (marks on prey, video observation, visual observation, list of potential predators). The main response variable was predation rate. Survival rates were converted to predation rates by subtracting the measured survival rate from 100% survival. Mean predation rates, their variance and sample sizes were extracted, or calculated from the figures (see Table S1). To calculate the standardized mean difference, mean, variance and sample size are needed. If not presented, it was sometimes possible to calculate these values from the published data or measure from the figures using a computer program. If only mean was available, we used it in calculating the unstandardized mean difference.

2.2. Statistical analyses

We calculated the effect size of urbanization on predation using two different methods, the standardised (Cohen's *d*) and the unstandardized mean difference (the latter with relative interaction intensity, *RII*, Armas, Ordiales, & Pugnaire, 2004). *RII* was also used because only 22 of the 35 datasets presented variance and sample size, which are needed to calculate the standardized mean difference, while *RII* can be calculated using means alone. Consequently, studies that did not report variance, but met all other criteria, could be included. Positive values indicate higher predation rates in rural than urban sites, while negative values indicate the opposite.

In small samples, Cohen's *d* tends to overestimate the effect size parameter (δ) (Borenstein, Hedges, Higgins, & Rothstein, 2009). We removed this bias by a correction that results in Hedges' *g* (Hedges, 1981). The summary effect size was computed using a random-effects model. We tested the publication bias numerically (Rosenthal's fail-safe number; Rosenthal, 1991) and statistically (Egger's regression test and trim and fill procedure) (Borenstein et al., 2009). Rosenthal's fail-safe number is able to calculate the number of unpublished, non-significant studies that need to be added to the study to change the outcome of the meta-analysis from significant to non-significant. If the fail-safe number is $> 5n + 10$, where n is the original number of studies, the outcome is robust (Rosenthal, 1991). To test if there was real bias, we used Egger's regression test with a mixed-effects meta-regression model. In case of significant asymmetry, Duval and Tweedie's trim and fill method (Duval & Tweedie, 2000a, 2000b) was used. This method identifies the number of missing studies, then these missing studies are added to the data set of the meta-analysis and the summary effect size is re-computed. We assessed whether effect sizes varied across studies (i.e., if there was heterogeneity) by using Q, the weighted sum of squares within a data set (Borenstein et al., 2009). The significance of