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# Categorizing wildlife responses to urbanization and conservation implications of terminology

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## Introduction

The study of urban ecology has emerged as a key element of conservation research (Miller & Hobbs 2002). Urbanization is a primary driver of habitat loss and fragmentation but also provides an opportunity to design and manage cities to retain biodiversity and facilitate interactions between people and the natural world (Miller 2005). As the field has developed, Blair's (1996) *avoider*, *adapter*, *exploiter* terminology has become the primary means of characterizing wildlife responses to urbanization. These terms, which were further developed by McKinney (2002), have provided a useful framework for studying urban ecology since 1996. However, we believe this terminology has shortcomings that obscure ecological mechanisms that affect urban biodiversity. We describe the limitations of this framework and offer a modified set of terms to advance urban wildlife conservation.

## Problems with Current Terminology

Blair (1996) defines *urban avoiders* as species that "reach their highest densities at the most natural sites." This group includes species that strictly avoid developed areas and those that occur in lower densities in developed relative to natural areas. Yet mechanisms that constrain the distribution and abundance of these 2 groups may be quite different. Distributions of strict avoiders are driven by their perception that developed areas are unsuitable (e.g., Acadian Flycatcher [*Empidonax virescens*] [Rodewald & Shustack 2008]) either because these areas are unsuitable or because avoiders erroneously perceive them to be unsuitable (Patten & Kelly 2010). In contrast, the abundance of species occurring in low numbers in developed relative to natural areas is controlled by factors that limit population size (e.g., top–down control, competition), although abundance may also be constrained by misperceptions that habitat quality is poor (Patten & Kelly 2010). Thus, strict avoiders and species occurring in lower numbers in developed areas should be separated into different categories.

Urban adapters (originally termed *suburban adaptable*) are most abundant in moderately developed areas (Blair 1996; McKinney 2002). This definition is problematic because of potential mismatches between density and habitat quality (Van Horne 1983). Despotic distributions (i.e., dominant individuals displacing subordinates into suboptimal habitat) or ecological traps can result in high densities of individuals in poor-quality habitats (Inman 1990; Battin 2004). As a result, higher densities in moderately developed habitats do not necessarily indicate stable or growing populations. Thus, categories should be defined based on population dynamics relative to urbanization rather than changes in density patterns. A second problem is the difficulty of quantifying *moderately developed*. Urbanization is measured in myriad ways, and moderately developed could vary depending on the metric used and range of urbanization (McDonnell & Hahs 2008). Therefore, categories should be based on clearly defined descriptions of urbanization that are applicable to the diversity of landscapes undergoing urban development.

Urban exploiters reach their greatest densities in highly modified habitats (Blair 1996). Like urban adapters, these species utilize anthropogenic resources to reach high densities in developed areas (McKinney 2002). Because population sizes of adapters and exploiters are linked to

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developed areas, both could be considered subgroups of a single category in which developed areas affect population dynamics.

## Revised Terminology and Conservation Implications

We propose a modified set of terms based on differences in population dynamics in developed and natural areas. We define *developed* and *natural* in this context and justify their use as the basis for our categorizations of wildlife responses to urbanization. We refine the definition of *urban avoider* and replace the terms *exploiter* and *adapter* with *urban utilizer* and *urban dweller*. These categories do not address habitat selection during migration or natal dispersal because habitat use during these periods is often more variable than in the breeding and nonbreeding seasons (Moore et al. 1995).

To standardize the descriptions of urbanization used to categorize wildlife responses, we propose a binary system of natural and developed. Natural areas are minimally modified (if at all) for human use (e.g., restored areas, habitat remnants), whereas urban developed areas have been substantially altered for residential, recreational, commercial, or industrial purposes. (We did not consider other forms of development such as agriculture.) These terms are broadly applicable to landscapes regardless of differences in the extent or intensity of urbanization and reflect fundamental differences in the way species respond to urban development.

We restrict the category urban avoiders to species that rarely occur in developed areas (e.g., mountain lion [*Puma concolor*] [Gehrt et al. 2010]). Although such species are generally absent in developed areas, they may persist in natural areas embedded in urbanized landscapes (Markovchick-Nicholls et al. 2008). Consequently, conservation of urban avoiders in cities depends on the size, shape, number, configuration, quality, and connectivity of natural areas in the urban matrix (Savard et al. 2000; Donnelly & Marzluff 2004).

Our definitions of *urban dweller* and *urban utilizer* are based on the relative importance of natural and developed areas to population dynamics. Persistence of urban dwellers in an urbanized landscape is independent of natural areas (i.e., population growth rates $\geq 1$ regardless of immigration from natural areas; for example, orb-weaving spider [*Nephila plumipes*] [Lowe et al. 2014]). Urban utilizers occur in urban environments as nonbreeders (i.e., in the nonbreeding season or as foragers only) or as breeders that are present only because of dispersal from adjacent natural areas (e.g., northern brown bandicoot [*Isoodon macrourus*] [FitzGibbon et al. 2007]).

The distinction between urban dwellers and urban utilizers is crucial from a conservation perspective. Because the persistence of urban dwellers is independent of natural areas, they are unlikely to be extirpated from urbanizing landscapes. This does not mean, however, that they are present in all types of developed areas. Managing urban dwellers requires altering habitat in the urban matrix by manipulating factors that limit population size in different types of developed areas—either to increase numbers for species that are of conservation interest or to control populations of pest species. In contrast, conservation of urban utilizers depends on both developed and natural areas. Their persistence in urbanizing landscapes is contingent on management of natural areas, and their abundance in developed areas is influenced by the management of limiting factors in those environments. Research on the conservation of urban utilizers has the greatest potential to increase biodiversity in developed areas because manipulation of factors that control populations may facilitate greater use of urban areas.

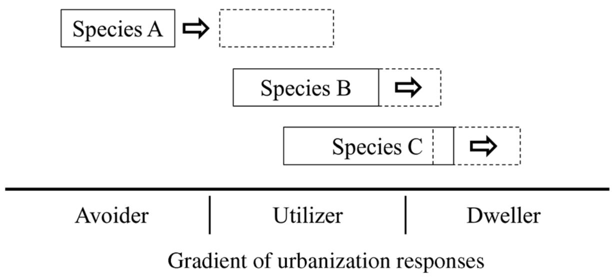


*Figure 1. Hypothetical species responses along the gradient of urbanization responses. Avoider, utilizer, and dweller represent portions of this gradient. The range of population responses for a particular species (solid lines) can be fully contained within a particular category (e.g., species A and B) or span multiple categories (species C). Shifts in population responses to urbanization that change the range of responses for a species (dashed lines) may transition a species from one category to another (species A), broaden the range of responses so a species is characterized by multiple categories (species B), or shift a species from multiple categories to a single category (species C). Shifts in responses could occur in either direction (arrows) along the gradient of responses, but only examples that improve urban biodiversity are shown.*

The terms *urban avoider*, *urban utilizer*, and *urban dweller* form a gradient of responses to urbanization, with each category representing a portion of that gradient (Fig. 1). Urban avoider populations vary from extirpated in developed landscapes to self-sustaining in networks of natural areas embedded in an urban matrix. Urban utilizers range from making occasional use of urban resources to breeding in developed areas. Urban dwellers vary from having viable populations in both natural and developed areas to being entirely dependent on developed areas for survival. Within a species, population responses to urbanization occupy a range along the gradient of responses to urbanization. This range may be entirely within a single category or it may span more than one. Such variability in population responses could be produced by many factors, including differences in landscape characteristics, development histories, management practices, community composition, and genetics among populations. Ranges of responses can also change through time. Urban development alters how natural selection affects wildlife (Fischer et al. 2012), which can lead to rapid evolution (Badyaev et al. 2008), and behavioral flexibility allows some species to make use of previously overlooked resources (Tuomainen & Candolin 2010). Such evolutionary and behavioral changes can alter population responses to urbanization. For example, the Northern Goshawk (*Accipiter gentilis*) is an urban avoider throughout most of its range, but in the last half century it has colonized several European cities (Rutz 2008).

Variability in population responses and the potential for changes in these responses have important conservation implications for urban landscapes. Management actions and policies have the potential to improve habitat, which could shift a population from one category to another, broaden the range of responses for species, or shift the ranges along the gradient of response to urbanization. Such changes could ultimately lead to increases in urban biodiversity. This biodiversity potential—the difference between present and future diversity of a city—means that urbanized landscapes may become increasingly important to conservation efforts as populations of more species become urban utilizers and urban dwellers (Walk et al. 2010).

Our terminology improves on the avoider, adapter, and exploiter framework by clarifying the ecological differences underlying categories of urbanization response and how these differences apply to urban wildlife conservation. Our intention is that these terms will focus future research and conservation efforts on changing wildlife responses to urbanization so that the biodiversity potential of cities can be realized.

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