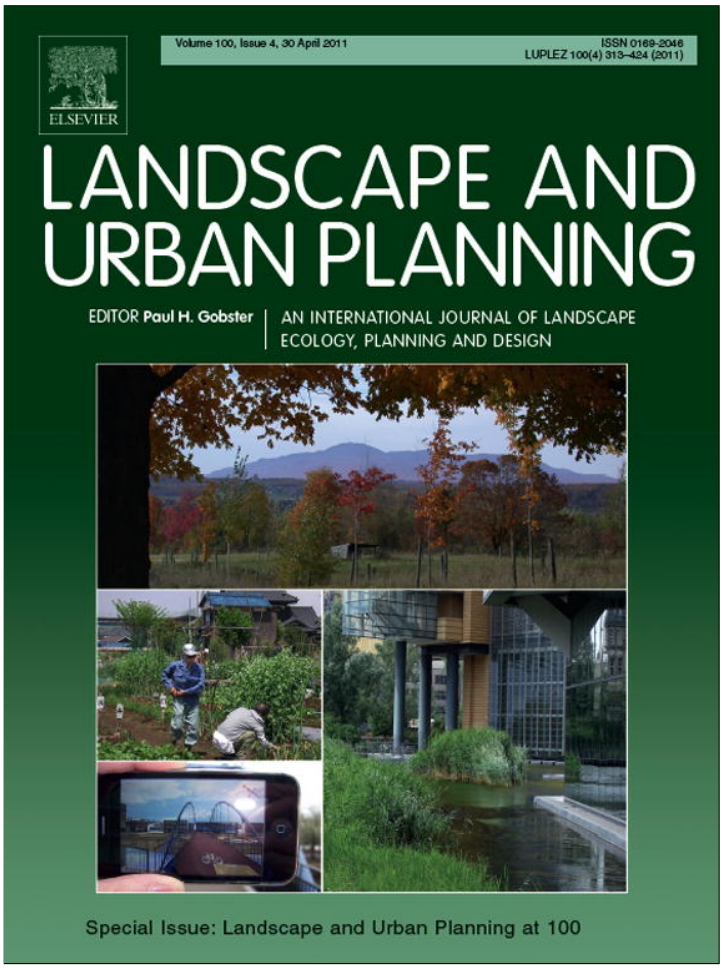

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Merging wildlife community ecology with animal behavioral ecology for a better urban landscape planning

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ABSTRACT

Cities are extremely human-modified environments, with few existing original habitats. Local, regional and global studies have indicated scale-dependent patterns of communities in relation to urbanization. In general, species with high abundance in urban environments are generalist species, whereas specialists have declined. However, these results do not indicate directly if urban habitats are either sink or source habitats for wildlife. Reproductive success, mortality, and dispersion are key factors to improve our understanding of how to support more diverse animal communities in urban environments. We need more research on the factors affecting the behavioral responses to urbanization of species with different life-histories. Some studies have demonstrated that urbanization has clear impacts on the behavior of wildlife species, a character that is strongly related to the success of species in a given habitat. Indeed, animals can adapt to urban ecosystems behaviorally, for example, by adjusting their food preferences, foraging behavior, anti-predator behavior, or extending the length of their reproduction season. Merging community and behavioral ecology will enable a more effective conservation of remnant semi-natural habitats in urbanized landscapes.

Cities represent the extreme of human-modified environments, with only remnants of the original habitats existing. Generally, urbanization decreases species richness and, correspondingly, biodiversity. Specialist animal species decline in urban areas, while generalists thrive. However, results obtained from different scales, biotopes and landscapes might differ, indicating scale- and habitat-specific behavioral response of individuals, populations and species on urbanization. For example, globally, urbanized landscapes are surprisingly diverse in their bird biodiversity (Pautasso et al., in press). High dominance of a few species and low species richness cause homogenization of communities across urban environments (Clergeau et al., 2006). Therefore, green areas in urban environments are relevant for biodiversity conservation and environmental awareness (Fernández-Juricic and Jokimäki, 2001). Because of the increasing rate of urban sprawl worldwide, it is important that both landscape planners and conservation biologists recognize the need to focus management efforts on urban biodiversity. Informed management decisions require more information about the factors affecting individual animals, their responses to humans, their breeding success and mortality, and movements across habitats (Marzluff et al., 2001; Ditchkoff et al., 2006). Urbanization affects the behavior of wildlife species too. Ideas of predator–prey interaction, foraging, sexual selection and network theories might also be relevant to use in an urban context. The purpose of this article is to (i) review some examples of recent studies of urban animals, with a main focus on birds, in the context of behavior ecology, (ii) call for a more mechanistic approach to achieve successful collaboration of behavioral ecologists with landscape planners and conservation biologists, and (iii) point out knowledge gaps and research opportunities.

Despite the high disturbance levels, there is evidence that species are colonizing urban environments, partly due to the milder microclimate, stable food resources, and putative low abundance of predators (Shochat et al., 2010). However, urban environments might also become an ecological trap for some species. Some factors (e.g. high abundance of winter food) might attract birds to settle in towns, but because of the low quality of food and corresponding

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low breeding output, the overall success of these species might be very low, although results are still controversial. However, more information about the spatial scaling of factors affecting breeding success and mortality in and around towns is necessary, because density estimates might be a misleading indicator of habitat quality and are highly dependent on the area over which they are estimated (Pautasso and Gaston, 2006). In addition, urban centers are not necessarily islands for animals; a city itself could affect the surrounding areas and *vice versa*.

Interestingly, wildlife can adapt to urban ecosystems behaviorally, for example, by adjusting their food preferences, foraging behavior, anti-predator behavior, or extending the length of their breeding season (Shochat et al., 2010; Rodriguez et al., 2010). Changes in foraging behavior, dietary habits, and temporal activity patterns have been noted both in birds and mammals living in urban environments (Ditchkoff et al., 2006; Møller, 2009). Urban colonizers generally adjust their responses to humans by tolerating closer approaches and becoming more dependent on anthropogenic food. This might change the intensity of inter- and intra-specific interactions, as well as the structure of animal networks. In addition, predators often follow the invasion of their prey to urban environments. For instance, avian nest predators, especially corvids, have benefited from urbanization and correspondingly decreased breeding success and density of ground-nesters in towns (Jokimäki and Huhta, 2000). In addition, some avian raptors, e.g. the Kestrel *Falco tinnunculus* and the Tawny Owl *Strix aluco*, have found new opportunities in urban environments by changing their main prey items from rodents to birds.

The changes in the behavior of species inhabiting urban areas require a deeper understanding of the proximate and ultimate factors behind the success and failure to colonize and persist in urban environments. Urbanization is expected to disturb communities (pessimistic theory) or communities may be able to adapt to urbanization (optimistic theory). Because of the high fragmentation of urban landscapes, species in these areas are forced to modify their spatial distribution to meet their life-history requirements. The ideas of foraging theories might be useful to apply when studying the role of patchily distributed food availability on urban wildlife. Also the ideas of sexual theories might be useful when dealing with success and failure to colonize and persist in cities. We propose that it is important to develop new models that capture the complex behavioral interactions (e.g., competition, predation, etc.) between humans and animals (e.g., responses to recreationists, collisions with vehicles, buildings, etc.) and between different animal species in urban habitats. These models can provide a strong theoretical framework to make testable predictions about the behavioral mechanisms underlying wildlife responses to urbanization. Understanding these mechanisms can enable us to better predict changes in biodiversity and restore some ecological processes in urbanized landscapes with the ultimate goal of increasing the species richness and reducing homogenization effects.

One example of this mechanistic approach comes from studies on strategies to encourage the coexistence of humans and birds in urban parks. From the perspective of suitable breeding habitat, urban parks can be considered high quality habitat fragments surrounded by a low quality urban matrix. However, these urban fragments are frequently crossed by pedestrians, who can decrease the spatial and temporal availability of resources for wildlife within the parks. The resource-use-disturbance-trade-off hypothesis captures these interactions by assessing the frequency of resource use by wildlife in relation to the frequency of human visitation to parks, assuming that birds react to human approaches at certain distances by leaving a suitable resource patch in a similar way to their response to predators (Fernández-Juricic, 2002). In general, animals may not be negatively affected with low pedestrian rates, as they can cope with reproduction and foraging needs in the intervals between pedestrians passing by. However, with high pedestrian rates, the intervals between pedestrians going by are substantially shortened, which may decrease the temporal and spatial availability of resources for animals. If pedestrian traffic is widespread across urban parks, this hypothesis predicts a reduction in densities and an increase in the probabilities of local extinction, which could lead to an ordered reduction in species richness depending on the susceptibility to human disturbance. These predictions have been corroborated in urban habitats. This mechanism gives us some tools to manage areas within parks to reduce the effects of human disturbance by determining the size of buffer areas for sensitive species and ranges of pedestrian rates that would minimize the negative effects of human disturbance.

Currently, we need a more mechanistic approach to studying the factors affecting colonization, persistence in urban habitats through human–wildlife interactions and species interactions, and dispersal through urbanized landscapes to improve the urban planning decision-making processes. By using individual marking of animals or by using radio telemetry technique, it might be possible to study dispersal of individuals within urban habitats as well as between urban environments and their surrounding rural areas. We suggest that urban animal ecological research can go one step forward by considering (i) biogeographical patterns in the behavioral features and species traits associated with urbanization success/failure, (ii) long-term population and individual level studies associated with behavioral ecological research to evaluate if and why urban habitats are either sink or source habitats for populations, and (iii) experimental landscape-scale studies of how different species are adapting to different levels of urbanization.

The rapid rate of urban sprawl can be considered an excellent opportunity to conduct replicated ecological experiments on a large scale to see how behaviors adjust to various degrees of environmental change. The study of urbanization covers many problems of adaptation in wildlife; e.g., increased competition within and between species where food distribution is patchy, and also the formation of new social networks among individuals and probably a rearrangement of (sub-) population structure. The theoretical frameworks and methods of behavioral ecology can certainly lead us towards novel insights in the field of urban ecology and the development of novel alternatives for the management and conservation of species in urban environments. For instance, individual-based approaches can enable us to connect individual behavior to population and community ecology from a theoretical point of view. Hypotheses and predictions can then be tested in the field and the lab while also taking into account the consequences for the long-term dynamics of populations in different urban contexts. We call for new interdisciplinary collaborations between urban ecologists and animal behavioral ecologists. This can be a productive endeavor that will bring novel insights for disease ecology, landscape genetics, wildlife management, and certainly urban ecology.

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