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Animal behavior in urban ecosystems: Modifications due to human-induced stress

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Abstract Wildlife-human interactions are increasing in prevalence as urban sprawl continues to encroach into rural areas. Once considered to be unsuitable habitat for most wildlife species, urban/suburban areas now host an array of wildlife populations, many of which were previously restricted to rural or pristine habitats. The presence of some wildlife species in close proximity to dense human populations can create conflict, forcing resource managers to address issues relating to urban wildlife. However, evidence suggests that wildlife residing in urban areas may not exhibit the same life history traits as their rural counterparts because of adaptation to human-induced stresses. This creates difficulty for biologists or managers that must address problems associated with urban wildlife. Population control or mitigation efforts aimed at urban wildlife require detailed knowledge of the habits of wildlife populations in urban areas. This paper describes the history of wildlife in urban areas, provides examples of wildlife populations that have modified their behavior as an adaptation to urban stresses, and discusses the challenges that resource managers face when dealing with urban wildlife.

Keywords Behavioral changes · Life history · Microevolution · Rural · Suburban · Urbanization · Wildlife

Introduction

Once considered to be suitable habitat for a small subset of wildlife species, urban ecosystems are now used by a wide array of wildlife that had previously been associated with rural landscapes or undeveloped wilderness. We have recognized that urban areas could serve as suitable habitat for species such as small mammals, birds, and herpetafauna: classic examples include the rock dove (*Columba livia*) and house sparrow (*Passer domesticus*). Numerous songbirds, squirrels, and other small to medium-sized mammals also have successfully acclimated to urban and suburban areas, in part because of their ability to use highly fragmented

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habitats. In recent decades, however, urban/suburban landscapes have been infiltrated by numerous other species (i.e., coyotes, *Canis latrans*; white-tailed deer, *Odocoileus virginianus*) that until recently, were considered to be intolerant of human activity. To most, the presence of wildlife in these settings provides immeasurable aesthetic value. However, the negative consequences of wildlife populations successfully residing and reproducing in close proximity to high human densities can be substantial.

Wildlife residing in urban landscapes pose considerable challenges to resource managers, biologists, and conservationists. Wildlife-human conflicts are rapidly growing in frequency, both as wildlife populations increase in number and suburban landscapes continue to sprawl from the urban epicenter. Humans residing in urban areas are less familiar with wildlife and how to deal with problems posed by wildlife than their counterparts 25–30 years ago. Additionally, suburban landscapes now often are designed to maintain a certain "rural quality" that was not practical 25 years ago. Rather than continuous rows of houses separated by concrete and manicured lawns, many new suburban areas are designed with larger lots such that houses are separated by trees and other native vegetation. This line-of-sight separation between homes creates wildlife habitat (travel corridors, hiding cover, forage, etc.) where little existed previously.

A common misconception concerning urban/suburban wildlife is that they are under less stress than their rural counterparts and the cruelties of nature are somehow buffered. This misconception may be based upon the belief that there are less predators in urban landscapes and that food is plentiful: it is rare that we witness predation or starvation in these landscapes. However, the reality is that individuals residing in these areas are exposed to a new array of stresses relative to their rural counterparts. These stresses, while different, impose substantial constraints on the biology of these animals, such that they may be forced to modify their behavior and life-history strategies to be successful. Often, stresses imposed on wildlife in urban ecosystems force animals to modify behavior in a manner that either avoids or mitigates the stress.

In recent years, the scientific literature has become replete with examples of wildlife species in urban environments modifying their behavior such that it differs from their rural counterparts. Behavioral or life-history modifications by urban wildlife may be related to movement, diet, reproduction, density, disease, and survival. Within this paper we will discuss patterns in behavioral modifications that have been reported for urban wildlife and describe how these modifications pose challenges to resource managers.

Behavior and life-history of urban wildlife

Movement and activity

Probably the most common example of behavioral modifications of urban wildlife due to anthropogenic stress is temporal variation in activity patterns. Human activity in urban areas tends to be greatest during daylight hours, causing some species to switch their activity to crepuscular periods, or in some cases to become strictly nocturnal. Large carnivores and other species that are easily disturbed by human activity commonly exhibit this behavior. McClennen *et al.* (2001), Tigas *et al.* (2002), and Riley *et al.* (2003) have reported that when large predators persist in an urban ecosystem, they adjust behaviorally to human activity through temporal avoidance. In essence, they reduce activity during daylight hours in urban settings compared with those in areas where human activity is minimal. While on the surface this may seem innocuous, if we assume that prey availability in urban areas is comparable to rural areas, then by restricting activity times during daylight hours, predators potentially may reduce their ability to locate and capture prey. This could have implications for diet, reproduction, condition, and disease prevalence.

Because of the high fragmentation of urban/suburban landscapes, many wildlife species in these landscapes are forced to modify their spatial distribution to meet their life-history requirements. In contrast to large predators, the raccoon (*Procyon lotor*) does not seem to exhibit temporal shifts in activity patterns (Prange *et al.*, 2004). However, food availability and distribution force this species to utilize the landscape in a much different pattern than its rural counterparts. Raccoons in urban areas exhibit an aggregated distribution that is focused on communal feeding sites. These sites are typically characterized by artificial resources such as parks and trash dumps. Additionally, the high concentration of artificial food sources cause home ranges to be smaller and population densities to be greater in mesocarnivores that readily forage on artificial food resources (Prange *et al.*, 2004; Smith and Engeman, 2002). Additionally, dispersal distances of juvenile wildlife may be less in urban areas than rural for many species because of low availability of suitable habitat and areas of high-human activity (e.g., U.S. interstates, dense human development) that impede dispersal (Etter *et al.*, 2002). These short dispersal distances may ultimately contribute to density issues.

Diet and nutrition

Shifts in behavior have been reported for some avian species with regards to foraging, which can have implications for other aspects of life history. Florida scrub-jays (*Aphelocoma coerulescens*) in suburban areas are more efficient foragers than scrub-jays in rural habitats (Fleischer *et al.*, 2003), likely because of access to human-provided food. Elevated availability of forage in urban areas due to human feeding (e.g., bird seed) may additionally influence reproduction. Some avian species, as well as mesocarnivores, that commonly consume foods associated with human populations can exhibit dramatic differences in their dietary habits. Human waste sites and roads provide substantial amounts of food in the forms of trash and road-killed animals. Animals in close proximity to these food sources commonly exhibit a marked increase in their consumption of these items (Prange *et al.*, 2004; Kristan *et al.*, 2004). These artificial concentrations of food can lead to density and disease issues, as was described with the raccoon (Prange *et al.*, 2004).

Reproduction

Dietary shifts have the potential to substantially increase population density if they result in nutritional increases. When nutrition improves, it is common for reproductive rates to increase, often resulting in greater litter sizes, greater survival of offspring, and ultimately greater densities (Robbins, 1993). However, urban stresses can have a multitude of unexpected influences on reproduction. Stresses associated with human disturbance, heat, noise, pollution, and other stimuli can influence reproductive characteristics such as timing of breeding, litter size, and mate acquisition. For example, scrub-jays in urban areas may commence breeding approximately 3 weeks earlier than normal. It is postulated that increased resource availability may serve as a perceptual clue for the appropriate timing of breeding (Fleischer *et al.*, 2003; Antonov and Atanasova, 2003). Elevated food availability in the form of bird seed and other anthropogenic sources is thought to be the cause of these breeding shifts.

Elevated noise associated with urban landscapes (i.e., vehicular traffic, factories) could negatively impact species that rely on vocalizations for communication. If excessive background noise reduces effective communication distance, reproductive success and other life history parameters could be negatively influenced. Estes and Mannan (2003) found that adult Cooper's hawks vocalized more in urban settings, which could have implications for strength of pair bonds and mating success. Similarly, Slabbekoorn and Peet (2003) found that great tits (*Parus major*) sing at higher frequencies at locations where urban noise (normally low frequency) could mask vocalizations.

Survival and mortality

Considering the differences between rural and urban environments with regards to food availability and the perceived differences in stresses, it is no surprise that there can be substantial differences in causes, timing, and rates of mortality in wildlife species that inhabit urban environments. For species that find greater food availability in urban environments, we would expect to find increased survival because in most cases greater nutrition leads to increased survival. However, not all species will find greater food availability in urban than rural areas, and not every example is quite so simplistic. Millsap (2002) describes survival of burrowing owls (*Athene cunicularia*) along an urban-development gradient. He found an inverse relationship between adult and juvenile survival, where juveniles had greater survival than adults. This is opposite of what has been reported previously (Thomsen, 1971). Millsap (2002), postulated that high mortality of adults in urban areas created high opportunity for recruitment of juveniles.

Koenig *et al.* (2002) have reported that rates of mortality for some herpetafauna may be elevated in urban areas because of increased exposure to domestic predators (e.g., cats and dogs). Numerous studies have documented high predation rates by feral and domestic felines in urban areas on avian and mammalian species, as well as herpetafauna (Lepczyk *et al.*, 2003; Gillies and Clout, 2003). While densities of natural predators may be lower in urban areas than more rural habitats, actual predatory pressures may be greater in urban areas because of human pets. Additionally, mortality due to vehicular traffic may be greater in urban areas for many wildlife species because of elevated traffic and road densities (Forman and Alexander, 1998). Our own research with white-tailed deer suggests that patterns of mortality for fawns may differ in urban areas. Preliminary unpublished data suggests that coyote predation on neonatal deer in urban areas may exceed what is found in rural areas. Additionally, we have documented a high rate of abandonment, possibly due to increased human disturbance. Etter *et al.* (2002) reported that mortality patterns for adult deer in urban areas differs from rural areas. Because deer in urban areas are not normally exposed to hunting pressure, their survival tends to be greater: the major cause of mortality is deer-vehicle collisions.

Disease and pollution

As mentioned previously, densities of wildlife in urban areas can exceed that found in rural areas. Raccoons and other species capable of foraging on human waste and road-killed animals often find greater availability of food in urban areas, leading to higher survival. However, these increased densities, in addition to causing greater wildlife-human conflicts, can lead to increased rates of disease transmission. As a result, prevalence of diseases in urban wildlife is sometimes greater than what is found in rural habitats. Avian roosts and artificial communal feeding locations for both mammals and birds additionally serve to concentrate animals in urban areas, and the potential for disease is a legitimate concern (Smith and Engeman, 2002; Johnson and Glahn, 1994). Additionally, the manner in which urban habitats alter the behavior of wildlife can increase susceptibility to disease. Cooper's hawks (*Accipiter cooperii*) in urban areas were found to deliver approximately twice the amount of prey to nestlings as rural hawks (Estes and Mannan, 2003). However, the authors found that nestling mortality was greater in urban areas due to an avian disease associated with the types of prey secured by adults.

Pollution associated with urban development can also have detrimental effects on urban wildlife. Several studies have documented increased lead concentration in urban wildlife (Raymond and Forbes, 1975; Getz *et al.*, 1977). If we refer to information published on human exposure to pollutants (Schell and Denham, 2003), it is conceivable that wildlife in urban settings may be coping with substantial physiological stress that could manifest itself through impaired reproduction, immune health, and survival. The physiological implications of this exposure for reproduction and survival in wildlife are largely unknown. Chandler *et al.* (2004) also found lead in urban wildlife, with greater levels of lead in urban house sparrows (*Passer domesticus*) than rural. They postulated that these high lead concentrations could have adverse effects on predators such as small falconiformes due to bioaccumulation. Dip *et al.* (2003) found high concentrations of organochlorine pollutants in urban red foxes (*Vulpes vulpes*). However, they documented that this resulted in high levels of mortality among adult males but not females. They indicated that females reduce their loads of these pollutants by passing it to offspring during lactation: males have no way of eliminating these pollutants from their system. While this maternal transfer of xenobiotics results in increased exposure to infants relative to adults, they did not comment on the effects on juveniles. Obviously, the effects of pollution on wildlife in urban environments can have harmful effects, but the manner in which they act upon a population will vary by species and pollutant.

Adaptation to urban environments

The above examples illustrate the manner in which wildlife species can modify behavior to successfully colonize urban/suburban environments. Human-induced stresses may cause these species to adapt to landscapes where traditional selection pressures (e.g., predation) may not be as important as in rural areas. As a result, wildlife populations that are confronted with novel human-induced stresses in urban environments may respond through rapid microevolution. Evidence suggests that selection can cause evolutionary shifts within a few generations (Rice and Emery, 2003; Reznick and Ghalamber, 2001). The first documented example of rapid microevolution of a species exposed to anthropogenic pressures is Kettlewell's report of peppered moths (*Biston betularia*) shifting color morphs in response to industrial pollution (Kettlewell, 1961). Although Kettlewell's report has received criticism for poor study design and hasty conclusions (Hagen, 1999), its implications for microevolution of species in rapidly changing environments are substantial. Since this original work, there have been numerous documented examples of rapid evolutionary response of populations exposed to human-induced environmental change in taxonomic classes including Oligochaeta, Insecta, Osteichthyes, and Aves (Rice and Emery, 2003; Diamond, 1986; Ashley *et al.*, 2003).

Losos *et al.* (2001) found rapid microevolution of *Anolis segrei* lizards introduced to the Bahamas. In less than 15 years, this species exhibited adaptive microevolution to vegetation differences between their new habitats and those in which they had evolved. In the Bahamian introduced populations, *A. segrei* uses perches of a more narrow width (e.g., vegetation width) than in their native habitat. Researchers found that hind length was significantly shorter in the Bahamian population than in the source population. Whether these changes were plastic in nature, or had a genetic basis was unknown. Able and Belthoff (1998) similarly found rapid evolution in the house finch (*Carpodacus mexicanus*). In the 1960s, approximately 20 years after being introduced to the eastern United States from California, this species displayed a dramatic shift in migratory behavior. House finches in California are almost completely sedentary. However, within 20 years of introduction, 36% of house finches in eastern North America were performing migratory movements of more than 80 km. In succeeding years, this proportion has fluctuated from 28–54%. Unlike the *Anolis* example, the house finches did not display any morphological adaptations. However, both cases seem to be evolutionary responses to local environmental variables that are designed to improve survival and ultimately fitness.

Resource managers and urban wildlife

As species are exposed to anthropogenic stresses that differ from the selective pressures under which they evolved, they may modify their behavior, or other life-history traits to be successful. Individuals most successful in adapting to new selective pressures likely will have the greatest reproductive success, leading to changes in morphological, behavioral, and genetic characteristics of the population over time. This shift in population structure, or behavioral characteristics may have direct consequences for control, mitigation, or management of species that consistently cause wildlife-human conflicts at the urban/rural interface. While our understanding of the biology of many of these species has been developed by examining populations of rural wildlife, wild populations that have adapted to human populated areas may not exhibit traits with which we are familiar. As a result, our control or management efforts for urban wildlife may not be entirely effective because they may be based upon incorrect data.

An example of how a comprehensive understanding of behavior and life history characteristics of urban wildlife is necessary for resource managers can be seen in the European starling (*Sturnus vulgaris*). Unlike rural starlings, urban starlings tend to demonstrate high affinity for nocturnal roost sites (Johnson and Glahn, 1994). This behavioral difference can have a significant influence on how resource managers deal with problematic roost sites in urban settings. In rural areas, staging area baiting with toxicants normally meets with limited success because the birds may not roost in the same area each day, and resource managers must employ a variety of damage control techniques to meet their goals. However, due to high site affinity of urban starlings for roost sites, staging area baiting can be an effective technique for reducing roosting starling populations in urban areas (Johnson and Glahn, 1994). While this example is a simplistic case of where differences in the biology of urban and rural wildlife influence management of wildlife in urban settings, it does effectively illustrate the need for detailed biological and life-history data of urban wildlife.

With increasing numbers of wildlife-human conflicts in urban areas, and increasing numbers of wildlife species that inhabit semi-urban/suburban areas, it is essential that we develop a better understanding of urban wildlife. Undoubtedly, the biology and life-history of urban wildlife can differ substantially from rural populations of the same species, whether due to behavioral or morphological plasticity, or genetic microevolution. While the presence of wildlife in urban areas is nothing new, the increased need for wildlife management in urban areas is somewhat novel. For this reason, science is lagging. Until our understanding of these urban residents is as complete as our understanding of their rural counterparts, we will continue to encounter difficulty when managing wildlife in urban settings. Essentially, we may need to re-evaluate the biology of these animals in urban/suburban areas to effectively mitigate their effects on society.

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