Investigating the welfare of wild animals in urban environments

Animal Ethics

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4200 Park Blvd. #129
Oakland, CA 94602
United States of America

info@animal-ethics.org
www.animal-ethics.org

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This report was completed by Amber Ross based on research by Elisabeth Dimitras, Amber Ross, and Sarah Stegeman.

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Introduction

The welfare of wild animals has so far received little attention in the scientific literature, particularly concerning wild animals living in urban environments. While there has been an increasing amount of research regarding urban wild animals over the last few decades, it has primarily been focused on the topics of animal behavior, conservation, landscape ecology, wild animal management, and population ecology. Few of these studies have considered the wellbeing of urban animals, but information from this research can be used to consider the ways in which urban wild animal welfare may be impacted.

Objectives and methodology

This review aims to gain a better understanding of what the lives of urban wild animals are like and the factors that may positively or negatively affect their welfare. This information can then be used to devise ways of improving overall welfare and reducing suffering in urban wild animals. We will also present ideas regarding future research that could inform the development of a new research field called urban welfare ecology.

We conducted a review of publications on urban wild animals from various fields to investigate how the welfare of these animals may be impacted. Definitions of the term “urban” vary within the existing field of urban ecology, and we have specified the types of urban areas and degrees of urbanization as they have been described in the literature. We consider the general term “urban” to refer to areas occupied by humans that have a relatively high cover of buildings and infrastructure, primarily cities, suburbs, and industrial areas.

Population dynamics

The characteristics of urban wild animal populations were examined to identify patterns and trends. We found that many wild mammals and birds have high survival rates, early and prolonged breeding seasons, high population densities with small territories, and reduced migration in urban environments. Factors that have likely contributed to these trends include high resource availability due to food subsidies, low rates of predation, warm climates from urban heat island effects, and the tendency of many urban animals to adopt more sedentary lifestyles and have slower life strategies.

Behavior

Increased intraspecific aggression has been observed in some urban animals, which may be due to high population densities and competition for better quality resources. Interspecific competition for resources may also increase among urban species with similar diets. Birds were found to be more social in urban areas, which may be advantageous as it helps individuals find new food sources, compete with other species, and detect threats. Some urban animals display low vigilance behavior, which is believed to be the result of low rates of predation and becoming accustomed to the presence of humans. However, the masking effect of urban noise can reduce the ability of some animals to detect a potential threat, and they may compensate for this by increasing their vigilance behavior.

Harms facing urban wild animals

The conditions of urban environments leave wild animals vulnerable to a number of different harms. Increased competitive behaviors in urban animals are likely to result in higher instances of injuries, mortalities, and weak body conditions in some individuals. High densities and increased contact between individuals can lead to high transmission rates of diseases and parasites in populations. Transmission rates can also be influenced by the nutritional quality of supplemental food and lighting patterns in urban environments. Survival rates are high in many urban animals, but this can result in more aging animals with the potential to develop cancer. While warm urban temperatures can be beneficial during colder months, urban heat island effects can intensify extreme heat events, increasing the risk of dehydration, mortalities, and poor welfare in wild animals.

Five animals commonly found in urban areas

To gain further insight on the factors affecting urban animal welfare, case studies were conducted on five wild animals that are commonly found in urban environments: *Apodemus agrarius* (striped field mouse), *Passer domesticus* (house sparrow), *Columba livia* (urban pigeon), *Pteropus alecto* (black flying fox), and *Iguana iguana* (green iguana). Although these case studies were limited by the amount of information available in the reviewed literature, we found that an individual animal's welfare was influenced by many factors, including their life history, physiology, behavior, and susceptibility to particular harms.

Green iguanas, for example, have become increasingly abundant in urban areas of Florida. They are ectothermic reptiles who depend on environmental temperatures to regulate their body temperature. In cold temperatures, they may become lethargic and cold-stunned, and prolonged exposure to cold can result in death. There have been many reports of cold-stunned iguanas lying immobile or falling from trees in urban areas of Florida during periods of cold weather. There is a high risk of injuries and mortality when they fall, and they are extremely vulnerable to other harms while they are unable to move. If they recover from a cold-stunned state, they may still experience health problems, decreased fitness, and reduced territorially and breeding behaviors afterward, which can have long-term effects on the iguana populations.

Helping urban wild animals

We recommend that the wellbeing of wild animals should be taken into account when designing, constructing and managing urban areas. Providing resources such as artificial shelters can offer animals protection, and additional water sources can reduce cases of dehydration and mortality in extreme heat events. Vaccinating wild animals can reduce cases of disease, and contraception can reduce transmission rates by lowering the number of individuals in a population. Reducing the size of populations through contraception can also reduce suffering in populations where individuals experience poor welfare. Public awareness and education can improve the welfare of urban animals by encouraging people to assist animals in need of help, and generating long-term support for policies and organizations that aim to improve animal welfare.

Future studies

Many studies of urban animals have so far been limited by the number of species and types of areas being researched. Due to the heterogeneity of different urban areas, and the variation in responses of different animals to these environments, the findings of such studies many only be relevant in specific contexts. Future studies of urban animals would benefit from collaborating with different researchers to build datasets on multiple species in a range of different urban environments. These datasets can then be used to form theories and models related to urban animal welfare, and help develop plans and policies to reduce suffering of urban animals. Future studies in the developing the field of urban welfare ecology would aim to assess the welfare of individual animals, as well as the impact that their presence has on the wellbeing of other animals in the area. We could then evaluate how the presence of animals of a particular species contributes to more or less suffering, and use this information to develop effective ways to improve the overall welfare of all animals in urban environments.

Introduction

The welfare of individual urban animals has so far received little attention in the scientific literature. However, work focused on the situation of animals can draw on information from previous research to better understand the lives of wild animals in urban environments and the factors that affect their wellbeing (Animal Ethics 2020a).

A review by Magle et al. (2012) found that urban wild animal research has increased over the last few decades (Fig. 1), but at the time still represented less than 2% of publications in scientific journals, despite the global acceleration of urban growth. Of these studies, the majority focused on mammals and birds (Fig. 2), and were related to the topics of animal behavior, conservation, landscape ecology, wild animal management, and population ecology. Many studies have also focused on the evolution and ability of animals to adapt to urban conditions, known as synurbization (Gliwicz et al. 1994; Luniak 2004; Parker & Nilon 2008; Birnie-Gauvin et al. 2016; Pieniążek et al. 2017).

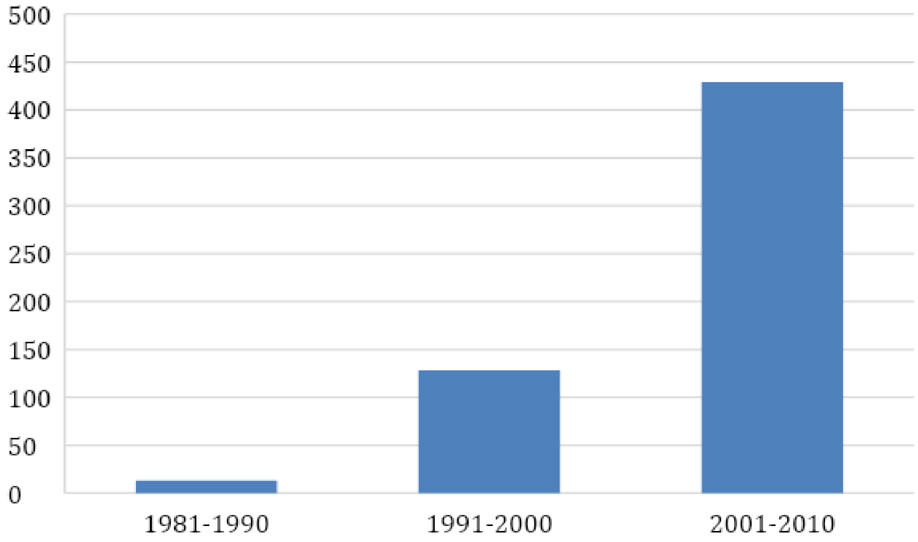

Figure 1. Number of urban wild animal research publications by decade. Based on data from Magle et al. (2012).

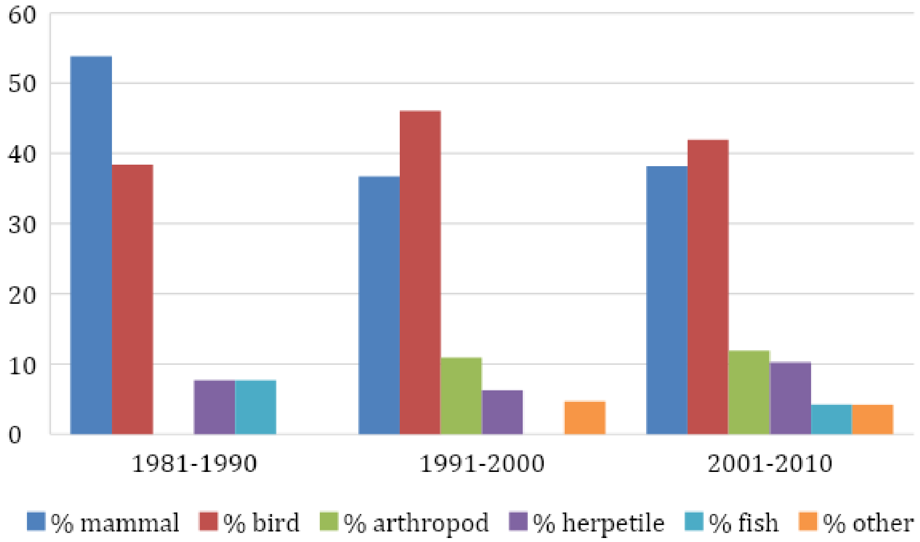

Figure 2. Percentage of different taxonomic groups that were the focus of urban wild animal research publications by decade. Based on data from Magle et al. (2012).

This report reviews a number of studies from a variety of scientific fields to investigate ecological patterns and trends in the lives of urban wild animals, and the ways in which their welfare may be positively or negatively impacted. We further examine how an individual animal's welfare may be influenced by factors such as their life history, physiology, and behavior, using case studies of five wild animals who are commonly found in urban areas. We also discuss ways we can improve the lives of urban wild animals, not just by reducing harm but also by taking actions that will benefit them, and we present ideas regarding future research in this field, which can be called *urban welfare ecology*.

Methodology

Publications from various fields were reviewed to collect information about population dynamics, life history traits, behavior, and other factors that could affect the wellbeing of animals living in urban areas. Literature searches were targeted using the term "urban," and publications were reviewed for suitability of inclusion based on study locations and the types of animal populations that were researched.

Urban ecology is an existing field that focuses on the distribution, abundance, and interactions between organisms living in urban areas (Pickett 2001; McDonnell 2011), and is distinct from the proposedemerging field of urban welfare ecology, which would focus on the wellbeing of wild animals in urban environments. There are many different interpretations of the term "urban" within the field of urban ecology (MacGregor-Fors 2011). Researchers have considered a number of different factors to determine whether an area is considered urban or not, including the population size or density of humans in the area (Rubbo & Kiesecker 2005; U.S. Census Bureau 2020), the degree of land covered by buildings and infrastructure (Møller 2009), or a combination of these factors (Niemelä 1999; Shochat et al. 2006; Johnson & Munshi-South 2017). Due to the heterogeneous nature of urban areas, many studies discuss them in the context of an urban gradient, ranging from heavily urbanized areas with high densities of human populations, buildings, and infrastructure, to areas with relatively little human activity or alteration (Table 1) (Gering & Blair 1999; Sepp et al. 2017; Bateman & Fleming 2012).

Table 1. Variations in the degree of landscape features along an urban gradient, from highly urbanized city centers to undeveloped areas with relatively little or no urbanization. Adapted from Bateman & Fleming (2012).

	City centers	Suburbs & industrial areas	Towns & villages	Rural farmland	Undeveloped areas
Human density	●●●●	●●●	●●	●	
Trees & vegetation	●	●	●●	●●	●●●
Buildings & infrastructure	●●●●	●●●	●●	●	
Altered climate	●●●	●●	●		

In this report, where possible, we have specified the types of urban areas being discussed, or the degree of urbanization along an urban gradient, based on the information available in the scientific literature. Where the general term "urban" is used, we are referring to human-occupied areas with a relatively high degree of land covered by buildings and infrastructure, primarily cities, suburbs, and industrial areas.

Population dynamics

The characteristics of populations and how they change over time can tell us much about the lives of the individual animals within them. Populations fluctuate in response to environmental conditions, and studies have shown that urban environments influence patterns of distribution and abundance in wild animal populations to varying degrees (Marzluff et al. 2001; Adams et al. 2005; Chace & Walsh 2006). Factors such as resource availability, climate, and disturbances such as fires and floods, can affect the survival rates, reproduction rates, and population densities. For example, when resources are abundant, populations will typically increase, as survival and reproduction rates tend to be high (Ridley 2004). An animal's life history, physiology, and behavior will also affect how they respond to these environmental conditions, and consequently, influence the population as a whole (Rodewald & Gehrt 2014). Here we will examine how urban environments influence population dynamics, and identify trends in urban wild animal populations.

Survival

Previous studies have found that many urban mammals have high survival rates, including fox squirrels (*Sciurus niger*) (McCleery et al. 2008), raccoons (*Procyon lotor*) (Prange et al. 2003), coyotes (*Canis latrans*) (Gehrt 2007), white-tailed deer (*Odocoileus virginianus)* (Etter et al. 2002; Lopez et al. 2003), and woodchucks (*Marmota monax*) (Hellgren & Polnaszek 2011). Studies have also found high survival rates in many urban birds, including blackbirds (*Turdus merula*) (Gliwicz et al. 1994), mockingbirds (*Mimus polyglottos*) (Stracey & Robinson 2012), and Florida Mottled Ducks (*Anas fulvigula fulvigula*) (Varner et al. 2014). A study of birds living along an urban gradient in Washington D.C., found that survival rates of northern cardinals (*Cardinalis cardinalis)* and gray catbirds (*Dumetella carolinensis*) increased as urbanization increased, while survival of American robins (*Turdus migratorius*) and song sparrows (*Melospiza melodia*) were highest when urbanization levels were moderate (Evans et al. 2015).

High survival rates in urban animals have been attributed to the high food availability and low rates of predation that are common in urban environments, as well as a tendency in many urban animals to adopt a more sedentary lifestyle (Adams et al. 2005; Gliwicz et al. 1994; Luniak 2004; McCleery et al. 2008; Sepp et al. 2017). Urban areas tend to have warmer temperatures than their surrounding areas, due to increased heat-absorbing surfaces and reduced canopy cover, known as the urban heat island effect (Oke 1995; Zipperer et al.1997). These warmer conditions may contribute to the high survival rates displayed by some urban animals during the winter months (Seress & Liker 2015), including fox squirrels (McCleery et al. 2008), opossums (*Didelphis virginiana*) (Kanda et al. 2009), and blackbirds (Gliwicz et al. 1994).

Reduced rates of predation and high resource availability are associated with slower life strategies, characterized by slow growth rates and development and longer life spans (Sepp et al. 2017). Slow rates of physiological aging and slow life strategies in mammals have been linked to low levels of predation (Austad & Fischer 1991; Austad 1993). This may be due to natural selection favoring traits that promote longevity in populations with low mortalities, while populations that suffer high mortalities at early ages are more likely to evolve traits that promote early maturation and high reproduction rates (Johnson et al. 2019). Slower life strategies are also observed in urban birds, who tend to have high survival and small clutch sizes, suggesting a higher investment in self-maintenance (Croci et al. 2008; Sepp et al. 2017). Urban birds tend to display little sexual dimorphism in their plumage coloration, which is also indicative of a higher investment in survival and less in reproduction (McLain et al. 1999; Croci et al. 2008). Urban birds have long life expectancies (Croci et al. 2008), and Evans et al. (2009) reported that there are many old animals of other species in urban environments.

High food availability in urban areas is due in large part to predictable food subsidies, such as bird feeders and discarded foods, which have been linked to improved individual fitness and population increases in certain animals (Oro et al. 2013). For some populations, there is a risk of becoming so dependent on supplementary food sources that they can no longer be sustained by natural food sources alone (Orell 1989; Martinson & Flaspohle 2003; Parker & Nilon 2008), while other animals have demonstrated little dependency on food subsidies. Brittingham and Temple (1992) compared a population of black-capped chickadees in an area where bird feeders had been present for the previous 25 years during winter, to a population in an area where feeders had never been present.

The results found there was no difference in survival rates during a winter when neither population had access to bird feeders, indicating that food subsidies did not affect the birds' ability to survive on natural food sources alone. The authors noted, however, that these were rural populations in areas of little disturbance, and that urban populations may have different levels of dependence if natural food sources are less abundant.

The results of Gering and Blair (1999) suggest that predation rates may be influenced by the level of urbanization in an environment, with predation decreasing as urbanization intensifies. City centers, for example, are likely to carry lower predation pressures than suburban areas. Predation accounted for less than 5% of urban fatalities in fox squirrels living at the campus of Texas A&M University, despite a large cat population in the area (Ash & Adams 2003; McCleery et al. 2008). Low rates of predation in urban environments have been attributed to the ability of some animals to adapt to urban conditions better than others (Luniak 2004; Shochat et al. 2006; Seress & Liker 2015). Some urban bird species have evolved traits such as loose tail feathers that allow them to escape more easily from predators (Møller et al. 2006). Certain urban animals may exhibit low predatory behavior if they rely more on supplemented food sources, as they will be less likely to expend energy on hunting (Prange et al. 2003; Gehrt 2007; Fischer et al. 2012).

Reproduction

Urban animals tend to have early and prolonged breeding seasons, which is thought to be facilitated by sedentary lifestyles and warm urban climate conditions (Luniak 2004; Rodewald & Gehrt 2014; Sepp et al. 2017). In certain urban animals, reproductive timing may also be influenced by body size (Shustack & Rodewald 2010), flexibility in gonad development and hormone secretion (Partecke et al. 2004), and artificial night lighting (Kempenaers et al. 2010). While some species may gain reproductive benefits from early breeding seasons (Perrins 1970; Verhulst et al. 1995), in other species, it seems to have no effect on their reproductive success (Shustack & Rodewald 2011; Aldredge et al. 2012). A meta-analysis of passerine birds found that birds in urban environments showed a pattern of early lay dates, but with low clutch sizes and low success of fledglings (Chamberlain et al. 2009). Morneau et al. (1995) found that American robins (*T. migratorius)* living in a dense suburb of Montreal had long breeding seasons, but also had the potential for large clutch sizes and high reproductive success. The authors suggested that this may be due in part to the abundance of favorable foraging sites in suburban environments, such as areas with short vegetation and exposed soil (Heppner 1965; Eiserer 1980).

In addition to prolonged breeding seasons, warmer climate conditions in urban environments may result in other increases in reproduction in certain animals. In wall brown butterflies (*Lasiommata megera)* living in central Belgium, larval survival was found to increase along an urbanization gradient in sites with a higher percentage of built-up areas, suggesting that warmer urban conditions had a positive impact on larvae development (Kaiser et al. 2016). In Sydney, Australia, the fecundity of orb-weaving spiders (*Nephila plumipes*) was higher in individuals living closer to the city and in areas with a higher degree of land covered by hard surfaces, indicating that their fecundity is influenced by warmer urban temperatures (Lowe et al. 2014).

Unique sites and structures found in urban environments may also contribute to high reproductive rates by providing animals with shelter and warmth in colder weather (Luniak 2004; Adams et al. 2005). Fox squirrels (*S. niger*) use buildings as safe refuges, and females use them to raise their young during late winter and early spring (McCleery et al. 2007). Animals may also learn through experience which urban sites are better suited to their reproductive needs. Northern mockingbirds (*Mimus polyglottos*) have been observed returning to urban nesting sites where they have previously had a successful breeding season, and avoiding sites where they experienced lower breeding success (Stracey & Robinson 2012).

The high resource availability found in urban environments is an important factor in animal reproduction. High reproduction rates in urban racoons may be a result of subsidized food sources (Rosatte et al. 1991). A review of studies on bird food provisioning made by Robb et al. (2008) found that, overall, supplemental food led to an earlier lay date in 57.6% of cases studied. For scrub-jays in urban areas, it is thought that high resource availability may serve as a perceptual clue for the appropriate timing of breeding (Fleischer et al. 2003; Antonov & Atanasova 2003). Food provisioning may allow breeding females to spend less time foraging, allowing early initiation of incubation, better protection of eggs from predation, and early fledging, resulting in better survival rates of chicks (Bollinger et al. 1990).

Densities

Animals who have become well-adapted to urban environments tend to have high population densities in small areas, with small individual territories for pairs and families (Gliwicz et al. 1994; Luniak et al. 1997; Marzluff 2001; Luniak 2004; Bateman & Fleming 2012). Factors contributing to high densities include low predation rates, high resource abundance, and limited space in urban areas (Luniak 2004; Shochat et al. 2004; Bateman & Fleming 2012). For birds living in European cities, population densities were found to be larger in species that have colonized urban areas over longer periods of time, indicating that animals who have undergone a gradual adaptation to urban environments may experience higher densities (Møller et al. 2012).

Population densities may be influenced by particular life histories and ecological traits. Animals with high densities in urban environments are often nonmigratory, with high fecundity and high dispersal capabilities (Kark et al. 2007; Croci et al. 2008; Møller 2009; Rodewald & Gehrt 2014). Generalist animals are also more likely to thrive in urban environments compared to animals with specialized diets and a narrow range of living conditions (Croci et al. 2008; Ordeñana et al. 2010). Larger mammals, such as bears and coyotes, typically have wide home ranges and smaller population densities, while smaller home ranges and larger densities are characteristic of smaller-bodied mammals, such as raccoons and opossums (Beckmann & Lackey 2008; Crooks 2002). The solitary nature of certain animals, such as bobcats and mountain lions, also contribute to lower densities (Crooks 2002).

Locations within an urban area and site fidelity may affect densities in some animals (Prange et al. 2003). For example, urban raccoons favor areas with trees, such as parks and residential areas, while open areas such as fields, industrial areas, and vehicle routes are used less often or avoided (Hoffmann & Gottschang 1977; Rosatte et al. 1991). These may create barriers that restrict the animals' movement through urban environments (Prange et al. 2003), resulting in higher densities within their favored sites. Magpies (*Pica pica*) are also likely to have higher densities in green urban areas, such as parks, where there is a higher abundance and choice of trees for nesting sites (Antonov & Atanasova 2002; Jokimaki et al. 2017).

Increased food availability in urban areas has been linked to increased population densities in many animals, as higher resources contribute to higher survival and reproduction rates (Fedriani et al. 2001; Parker & Nilon 2008; Bateman & Fleming 2012; Rodewald & Gehrt 2014). Food supplementation can also affect the behavior of some animals, and in turn affect densities through smaller home ranges, smaller space requirements, and increased immigration to urban areas (Marzluff & Neatherlin 2006; Rodewald & Gehrt 2014). For example, Wright et al. (2012) found that Virginia opossums (*Didelphis virginiana*) living in the city of Kirksville, Missouri, had small home ranges and utilized food subsidies. The authors also observed that individuals had large body masses, indicating that they had regular access to abundant subsidies, which likely allowed them to maintain small home ranges containing more individuals.

Migration

Reduced migration is observed in urban animals, and proportions of birds that are migratory have been found to decrease along an urban gradient as urbanization levels increase (Kark et al. 2007). Migratory birds that are found in urban environments, such as blackbirds, rooks, and mallards, tend to stay in their breeding grounds during winter, likely due to the warm climate conditions and high food availability in urban areas (Luniak 2004; Adams et al. 2005). Food subsidies may also be responsible for large-scale changes in migration strategies. It has been suggested that the northward expansions of wintering grounds for Northern cardinals (*Cardinalis cardinalis*), American goldfinches (*Carduelis tristis*), and Anna's hummingbirds (*Calypte anna*) in North America may be explained by the presence of bird feeders in urban areas (Brittingham 1991, in Morneau et al. 1999; Greig et al. 2017).

Several studies have found that urban environments are more favorable for sedentary animals than for migratory animals (McClure 1989; Dunford & Freemark 2005; Kark et al. 2007; Croci et al. 2008). Migrants may need time to adapt to new environments, whereas sedentary animals, who live in the same environment their entire lives, have had a longer time and more opportunities to adjust to urban conditions (Croci et al. 2008). It is therefore likely that sedentary animals have a better ability to compete for urban resources, such as foraging and nesting sites, compared to migrants (Jokimaki & Suhonen 1998; Kark et al. 2007). Urban birds also tend to have strong dispersal abilities, which has likely played a large part in their ability to travel long distances and successfully colonize urban environments (Møller 2009).

Migratory behavior in wild animals may also be affected by lighting conditions in urban environments. The spectra emitted by artificial light may disrupt migration patterns of salamanders, who are typically terrestrial as adults, but migrate to aquatic areas, such as ponds, lakes, and rivers in order to breed and lay their eggs (Wise & Buchanan 2006). Ambient lighting can influence the timing of emergence and migration in many salamander species (Anderson & Graham 1967), so the presence of artificial light at night may disturb these timing patterns and the orientation of migrating salamanders, potentially resulting in reduced size and survival of juveniles (Semlitsch 1987; Wise & Buchanan 2006).

Behavior

Interactions with other animals

High population densities combined with reduced space and territories have likely contributed to the increased intraspecific aggression that is commonly observed in some urban animals, such as blackbirds (Luniak 2004). A study of grey squirrels (*Sciurus carolinensis*) living in the city of Washington, D. C., found that as grey squirrels' population density increases, there is also an increase in aggressive intraspecific behaviors, such as chasing, biting, and rapid tail flicking (Parker & Nilon 2008). It has been suggested that high intraspecific aggression may be due to competition for resources, as previous research has shown that more food resources were obtained by more aggressive squirrels in urban environments (Williamson 1983). Since urban environments typically have abundant food resources, squirrels may be competing for access to better quality resources or preferred foraging sites (Koprowski 1994; Steele & Koprowski 2001; Parker & Nilon 2008).

Shochat et al. (2006) theorized that high population densities can also lead to increased interspecific competition for resources among urban species who have overlapping diets. As more animals are attracted to areas of high food availability, those that are more efficient at finding and consuming those resources are likely to have higher survival and reproduction rates. This may result in the crowding out and exclusion of urban animals that are less efficient at obtaining food. Case et al. (1994) observed in urban and suburban environments of the Pacific Islands, the common house gecko, *Hemidactylus frenatus,* outcompetes the mourning gecko, *Lepidodactylus lugubris*, for the same food resources, mainly due to the larger body size and more aggressive behavior of the common house gecko. The researchers found that the abundance of mourning geckos increased by nearly 800% in urban areas where common house geckos were absent.

Predictable food subsidies may affect competition levels in different ways. Oro et al. (2013) notes that sites with abundant subsidies, such as dumps, sustain a large number of species and individuals, and possibly reduce competition, as there is no need to scramble or interfere with others to gain food. However, the authors suggest that the congregated nature of certain food subsidies may result in higher levels of competition, particularly where animals have a limited amount of time to access these resources, such as landfill sites being covered by machinery and discarded food particles sinking in bodies of water. In these cases, the larger or more dominant individuals may displace or exclude the weaker competitors (Cortés-Avizanda et al. 2012).

The social behavior of birds when foraging may also be affected by food subsidies. Supplementary food reduced the degree to which varied tits (*Poecile varius*) joined mixed-species flocks (Kubota & Nakamura 2000), supporting the assumption that mixed flocking helps birds find food in times of scarcity. During winter, flocks of blackcapped chickadees defend foraging territories, although when food supplements are provided flocks frequently cross territorial boundaries to visit feeders (Wilson 2001). In other species, territorial behavior can increase with provisioning since the presence of accumulated or high-quality food allows birds to engage in costly resource defense behaviors. This is seen in Carolina wrens (*Thryothorus ludovicianus*) who, when they are provided food, spend more time defending territories by singing (Strain & Mumme 1988). In the case of small woodland passerines, high population densities at the end of winter could trigger competition for ecologically similar migrants returning to those areas during the breeding season (Clergeau et al. 1998).

Studies have shown that birds tend to be social in urban environments, spending more time with conspecifics at foraging, roosting, and breeding sites (McClure 1989; Kark et al. 2007; Croci et al. 2008). Increased social behavior is thought to be an advantage in urban areas, as being in a group increases the likelihood of finding new food sources, and successfully competing with individuals of other species for resources (Sol 2008). Social groups also allow individuals to learn advantageous behaviors from others, such as communication and predator avoidance, as more individuals have a greater probability of detecting threats and giving early warnings to the rest of the group (Kark et al. 2007; Croci et al. 2008; Parker & Nilon 2008). It has been suggested that overall, being social may enhance adaptability and survival in urban environments (Kark et al. 2007).

Vigilance

Reduced rates of predation and continuous exposure to humans in urban environments can result in low anti-predator and vigilant behavior in certain urban animals (Metcalf et al. 2000; Blumstein 2002; Lopez et al. 2003; Adams et al. 2005; Coss 1999; Anchor et al. 2002; Seress & Liker 2015). Low vigilant behavior can increase an animal's fitness through increased energy intake, body condition, and reproductive success, as less time being vigilant results in more time foraging (Lima & Dill 1990; Brown 1999). In 2009, McCleery found that fox squirrels (*S. niger*) living at the Texas A&M University campus tended to decrease their anti-predator behavior, not only towards humans but also in response to coyote and hawk vocalizations. This behavior may be transferred to other stimuli and may have a cost in the future, as it means they would be more susceptible to unfamiliar predators**.**

Coyotes are common in certain urban areas, and will often alter their behavior to avoid people, such as increasing their activity at night and avoiding areas of high human activity (Gehrt 2007). In colder weather, they may be more active during the day, and may approach more human populated areas in daylight where food resources are available (Baker & Timm 1998; Timm et al. 2004; Gehrt 2007). Baker and Timm (1998) speculate that certain populations of coyotes in urban and suburban areas of southern California have become less fearful of humans over several generations. Coyotes that spend more time in urban areas may become more accustomed to being in close proximity to people, and pass this adapted behavior on to their offspring. This is more likely to occur in areas where food resources are high and aggressive behavior from humans is low (Timm et al. 2004).

Vigilant behavior may also be increased under certain urban conditions. Urban noise can have a masking effect, which restricts an animal's ability to detect sounds, such as an approaching predator (Barber et al.; Merrall & Evans 2020). This may affect feeding and reproductive performance in some animals because the compromised ability to detect predators can be compensated by having a low threshold for response. This is called the "increased threat hypothesis," where chronic noise affects behavior by increasing the perceived level of threat (Owens et al. 2012). In song sparrows (*M. melodia*), the perception of a high predation risk (without predation) indirectly reduced their breeding success because it affected the time-activity budget of parents who spent less time provisioning their brood by being more vigilant (Zanette et al. 2011). Similar effects were found in house wrens (*Troglodytes aedon*) exposed to predator calls along an urban gradient in western Massachusetts, U.S.A., where the poor condition of nestlings was thought to be due to parents reducing their foraging time to avoid detection by predators (Grade et al. 2021). Merrall and Evans (2020) found that passerine birds living along an urban gradient in and around the city of Sheffield, England, increased their vigilant behavior and were more reluctant to visit supplementary feeding stations when exposed to urban noise, resulting in reduced feeding rates. These birds were also less likely to visit feeders and have lower feeding rates as the level of urbanization increased.

Harms facing urban wild animals

Wild animals are vulnerable to a variety of harms in urban environments, including injuries, poor health, diseases, parasites, and extreme weather conditions. We have seen that many wild animals have high population densities in urban areas, which can increase their susceptibility to certain threats. Large densities of urban animals have been associated with high rates of intraspecific (Luniak 2004; Parker & Nilon 2008) and interspecific (Case et al. 1994; Shochat et al. 2006) competition, and animals in dense urban environments are also likely to experience high rates of injuries and mortalities from aggressive competitive behaviors. High competition levels may also result in some individuals suffering from nutritional stress and weaker body conditions if they are unable to access sufficient or high-quality resources.

Diseases and parasites

Large population densities and increased contact between individuals may cause urban animals to experience high transmission rates of diseases and parasites (Bradley & Altizer 2007; Møller 2009; Hassell et al. 2017). High resource availability within a small area further increases the risk of transmission, resulting from larger aggregations of animals at food sources, especially when resources are clumped together (Wright & Gompper 2005). Transmission rates may also be elevated by high reproduction rates, as an increased number of juveniles results in a higher proportion of the population who are more susceptible to infections (Bradley & Altizer 2007). Warm temperatures, limited seasonal changes, and irrigation that are typically found in urban environments can promote the growth and survival of disease vectors and parasites and further increase the likelihood of transmission (Baker et al. 2002; Louis et al. 2005; LaDeau et al. 2015). Some urban animals display adaptations to the elevated risk of disease and parasite transmissions, such as enlarged immune defense organs in urban birds (Møller 2009), but many are still vulnerable to these harms.

The nutritional value of supplemental food may influence the susceptibility of urban animals to parasite infections. The feeding of Northern Bahamian Rock Iguanas (*Cyclura cychlura*) by tourists in the Bahama Islands with carbohydrate-rich foods, such as cereals and grapes, has been associated with poor nutritional status, and high endoparasite infection rates and burdens (Knapp et al. 2013). While some endoparasites are not considered harmful to the iguanas, heavy burdens can promote clinical disease (Diaz-Figueroa & Mitchell 2006; James et al. 2006). However, food subsidies with high nutritional value may improve the health of urban animals by reducing malnutrition and strengthening their immune defenses against parasite infections (Bradley & Altizer 2007).

In urban environments, artificial lighting can affect the sleep patterns of wild animals. It has been reported that suburban great tits (*Parus major*) sleep significantly less, wake up earlier, and spend less time in their nest-boxes when exposed to artificial lighting at night (Raap et al. 2015). Sleep duration is important to an animal's health, as consistent sleep patterns are associated with a stronger immune system (Bryant et al. 2004). Comparative analyses of different mammal species found that mammals who sleep longer exhibit stronger immune responses and lower levels of parasitic infections, which may be due to an increased investment in their immune systems when asleep (Preston et al. 2009). Dark-eyed juncos (*Junco hyemalis*) who were exposed to artificial light at night experienced heavier parasite loads and increased inflammation during the spring and fall, indicating that artificial night lighting caused chronic infection relapses during their reproduction period, when energy costs are high (Becker et al. 2020).

High mortalities in songbirds have been attributed to outbreaks of avian salmonellosis, which can quickly spread through high densities of birds congregating at feeders and perches (Gonzalez-Astudillo & Hernandez 2012; California Department of Fish and Wildlife (CDFW) 2021). A *Salmonella* outbreak that began in California in December 2020 resulted in sickness and death in many songbirds, including pine siskins (*Spinus pinus*), lesser goldfinches (*Spinus psaltria*) and American goldfinches (*C. tristis)* (CDFW 2021), and as of April 2021, the outbreak had spread to seven other U.S. states (Centers for Disease Control and Prevention (CDC) 2021). Infected birds may experience rapid and labored breathing, shivering, loss of coordination, diarrhea, vomiting, convulsions, fluffed or ruffled feathers, and lethargy, with most birds dying within 24 hours of infection (CWHC 2020; CDFW 2021). Salmonellosis can also cause severe inflammation and tissue damage of the esophagus, with birds becoming dehydrated and emaciated due to difficulties eating and drinking, eventually leading to starvation and death (Lawson et al. 2018; CWHC 2020). It is unknown where birds initially become infected with the *Salmonella* bacterium, but the likelihood of infection increases when coming into contact with sewage and contaminated areas (Gonzalez-Astudillo & Hernandez 2012).

West Nile virus (WNV) is transmitted by mosquitoes and causes high avian mortality in urban areas (Gibbs et al. 2006; Bradley et al. 2008; Hamer et al. 2011). Many types of birds are susceptible to the virus, and certain species, such as corvids (crows, jays, magpies), house finches (*Carpodacus mexicanus*), and house sparrows (*P. domesticus*) show particularly high levels of infection and mortality rates (Hayes et al. 2005). A review by Kilpatrick (2011) found that transmission of WNV in North American birds was highest in urban environments. Bradley et al. (2008) conducted a study of songbirds in the greater metropolitan area in Atlanta, Georgia, and reported a higher prevalence of antibodies to WNV as the level of urbanization in an area intensified. This may be partly explained by the abundance of mosquitos in urban areas, particularly in urban water systems, such as wastewater plants and sewers. Mosquito larvae were found in neglected swimming pools in Bakersfield, California, and may have contributed to an increase of WNV infections in the area (Reisen et al. 2008). It is also possible that the abundant food supplies in urban areas have contributed to better health in urban animals, and strengthened their ability to tolerate and recover from viral infections, resulting in higher antibody levels (Bradley & Altizer 2007; Bradley et al. 2008). In adult songbirds, the prevalence of WNV antibodies was higher relative to juveniles, which was likely due to their longer exposure time to the virus (Bradley et al. 2008).

The prevalence of certain diseases in urban environments may be underestimated for a number of reasons. Many diseases can only be detected through diagnostic tests and thorough examinations, so disease surveys based on clinical signs alone are likely to underestimate the number of cases in a population (Jackson et al. 1999). Sick animals are likely to be less alert and are more susceptible to other threats, such as car collisions and predation, and injuries from these secondary threats make it unlikely that the underlying illness will be detected. In a study of skunks, raccoons, and foxes living in Toronto, Rosatte et al. (1991) suggested that diseases, such as rabies and canine distemper, were the most likely factor limiting population growth in these animals, as food and habitat were not found to be limiting factors. The prevalence of disease was difficult to estimate, as many carcasses were too decomposed to be tested, so the cause of death could be determined in less than 50% of animals in the study.

Cancer

Senescence is common for humans and for animals kept in captivity as well as for domesticated animals, but is much less common for animals in the wild since death by other causes usually prevents survival to old age where the risk of cancer is greatest (DeGregori 2011). However, in urban settings low predation rates, high resource availability, and low stress levels result in higher proportions of aging animals with the potential to develop cancer (Partecke et al. 2006; Narayan & Vanderneut 2019; Sepp et al. 2019). Factors that may contribute to increased cancer rates in urban animals include changes in diet, high levels of chemicals, infectious agents, changes in light levels, and reduced genetic diversity in urban animal populations (Giraudeau et al. 2018; Sepp et al. 2019). The risk of developing cancer in different animals will likely vary depending on cancer defense mechanisms and their ability to cope with these associated environmental pressures (Sepp et al. 2019).

Extreme weather

While warm temperatures in urban areas may create favorable climatic conditions for certain animals, when regional temperatures are high, local urban heat island effects can further intensify extreme heat events (Pipoly et al. 2020). Continuous exposure to high temperatures can negatively affect urban animals in various ways, including dehydration, reduced body mass in adults and developing offspring (Pipoly et al. 2020), and reduced egg survival (Hall & Warner 2018). The city of Bengaluru, India, also experienced a series of days of extremely hot temperatures in 2019, in which many dehydrated birds fainted and fell from the sky, including black kites, parrots, parakeets, hummingbirds, crows, and pigeons (New Indian Express 2019).

Warm temperatures and abundant food resources in urban environments have contributed to high survival rates of animals during the winter months (Gliwicz et al. 1994; McCleery et al. 2008; Seress & Liker 2015), but urban animals are still vulnerable to illness and mortalities in extremely cold temperatures. The risk and severity of certain health conditions, such as respiratory diseases and viral infections, have been associated with colder temperatures in wild animal populations (Agha et al. 2017; Cohen et al. 2020). Rosatte et al. (1991) noted that the number of winter-related mortalities in skunks, raccoons, and foxes living in metropolitan areas of Toronto, Canada, are extremely difficult to estimate, as many animals suffering from winter-related deaths are likely to die in their dens.

In 2010, the metropolitan area of Perth, Western Australia, experienced severe thunderstorms with heavy rain, severe winds, and large hailstones, some of which measured over two inches in diameter (Australian Government, Bureau of Meteorology 2010). Saunders et al. (2011) reported that these hailstones caused the deaths of 57 Carnaby's black cockatoos (*Zanda latirostris*), and a further 24 cockatoos suffered from severe injuries, including soft tissue and skeletal damage, and many more were likely affected but not reported. The injured cockatoos were taken to rehabilitation centers, but 11 of them could not be released due to the severity of their injuries. Twenty-six of the birds who died, and eight of the injured birds, were found in a park located close to Perth’s central business district. Witnesses observed the birds roosting in trees where they were unprotected from the hailstones during the storm. Black cockatoos are large birds, measuring between 20 to 23 inches in length (Kaarakin Black Cockatoo Conservation Centre (KBCCC) 2021), and may be unable to utilize crevices in trees and buildings for shelter like smaller birds.

Five animals commonly found in urban areas

We have seen that animals who have become well-adapted to urban environments generally have high rates of survival, prolonged breeding seasons, and high population densities. This is largely attributed to the abundant food resources, warm climate conditions, and low rates of predation that are characteristic of urban environments. Urban wild animals also show a trend towards a more sedentary lifestyle, and will sometimes display high levels of intraspecific and interspecific aggression and low vigilant behavior. Urban stressors, such as high risks of disease and parasite transmission, extreme weather, and urban noise and light, can negatively impact the health and wellbeing of wild animals in these environments. While this information provides us with some insight into the wellbeing of urban wild animals, there are still many aspects of their welfare that require further investigation. An individual animal's welfare may be influenced by other factors such as their life history, behavior, physiology, past and present interactions with their environment and other animals, and their susceptibility to particular harms. Below, we will examine the lives of five animals that are commonly found in urban areas, and various factors that may influence their wellbeing. While many factors are likely to influence the welfare of these urban animals, the factors discussed here are limited to the information that was available in the reviewed literature.

Apodemus agrarius (striped field mouse)

Striped field mice are small rodents that are greyish brown in color, except for the prominent black stripe that runs down their spine, from which they get their name (Animalia 2020). There are 24 subspecies of striped field mice, with populations found throughout Central and Eastern Europe and Asia (Fig. 3) (Wilson & Reeder 2005; Kaneko et al. 2017 [2016]). They occupy a range of different environments, including forests, grasslands, fields, wetlands, and urban areas (Gliwicz et al. 1994; Kaneko et al. 2017 [2016]). Striped field mice have become well-adapted to urban environments, and in certain highly urbanized areas such as city centers, they are one of very few species present and typically dominate the rodent community (Andrzejewski et al. 1978; Sikorski 1982; Łopucki & Kitowski 2017).

Figure 3. Estimated global distribution of *Apodemus agrarius* (striped field mouse). Adapted from International Union for Conservation of Nature (IUCN) (2008).

Population dynamics

Pieniazek et al. (2017a) found that striped field mice living in the city of Warsaw, Poland had high numbers of sexually-active males in urban populations, as well as high numbers of pregnant and lactating females. Urban populations also have prolonged breeding seasons, sometimes into the winter months (Gliwicz et al. 1994; Luniak 2004). Sexually active urban males have been found to reach large body sizes (Pieniazek et al. 2017a), which may enhance their reproductive success, although males have also experienced high mortality rates at the end of their breeding season (Andrzejewski et al. 1978). This increased mortality is believed to be the result of exhaustion caused by increased interspecific competition between males for access to mates (Pelikan 1965, as cited in Andrzejewski et al. 1978), although there are no studies investigating the evidence for this in urban striped field mice.

Striped field mice achieve high population densities in urban areas (Andrzejewski et al. 1978; Liro 1985; Gliwicz et al. 1994), with higher densities observed in cities compared to those in suburban populations (Babińska-Werka et al. 1981). This is thought to be due to the absence of competitive species, low rates of predation, as well as reduced migration in urban field mice (Andrzejewski et al. 1978; Babińska-Werka et al. 1981; Gliwicz 1981). In the city of Warsaw, parks and cemeteries contained the highest densities of field mice (Babińska-Werka et al. 1979), which may be due to the presence of trees and hedges in these areas, where individuals tend to aggregate (Babińska-Werka et al. 1979; Andrzejewski et al. 1978). While individual space and territories may be reduced in highly urbanized areas, field mice are also able to utilize urban features for nesting sites and shelters, such as cracks in concrete structures, buildings, tombs, and under stones (Babińska-Werka et al. 1979; Gliwicz et al. 1994).

In Lublin, Poland, striped field mice were found to have large body sizes in urban areas (Lopucki et al. 2019). This is likely due to their diet, as urban field mice were found to consume high-calorie foods, such as tree seeds, as well as fat droplets, which may originate from supplemented food sources (Babińska-Werka 1981). The high abundance of food in urban environments means that the mice spend energy on gaining and maintaining body weight instead of competing with others for resources and avoiding predators while foraging (Łopucki et al. 2019). This has likely contributed to their high survival during the winter months (Andrzejewski et al. 1978; Babińska-Werka et al. 1981; Gliwicz et al. 1994), although there are no studies investigating the possible negative health effects of a higher-calorie diet in urban field mice.

Urban field mice exhibit limited migratory behaviors and juvenile dispersal, as abundant food availability and warm climate conditions in urban environments allow mice to survive in the same location throughout seasonal changes (Andrzejewski et al. 1978; Gliwicz et al. 1994). Movement may be restricted due to ecological barriers, such as rivers and urban infrastructure (Gliwicz et al. 1994; Gortat et al. 2015), although if green corridors are present, mice are able to utilize these to travel between fragments (Liro & Szacki 1987). This propensity towards a sedentary life has likely reduced instances of injuries and mortalities in individuals that would otherwise be sustained through more migratory behaviors, but there is no research regarding the extent of this.

Behavior

In addition to the generally good physical condition of striped field mice in urban environments (Krebs 2001), research shows that they have good mental condition as well. Striped field mice living in a Warsaw city park exhibited the same behavioral reactions to traffic noise compared to a non-urban population, which suggests they are well adapted to stress factors that occur in urban areas (Pieniazek et al. 2017b). Analyses of fecal samples from striped field mice living in the cities of Warsaw and Lublin, Poland, revealed low levels of the stress hormone corticosterone, indicating that they do not experience high levels of stress (Pieniazek at al. 2017b; Lopucki et al. 2019). This is thought to be the result of reliable and abundant food sources, and infrequent competitive behaviors (Lopucki et al. 2019). Urban field mice are not often exposed to multispecies communities where niches overlap and they must compete with others for resources, so they experience low interspecific competition pressure (Andrzejewski et al. 1978; Łopucki et al. 2019). The brown rat (*Rattus norvegicus*), for example, is a dominant murid species in urban environments, but prefers to occupy sites near buildings with abundant food subsidies over the green areas favored by field mice, which leads to a low frequency of stressful confrontations for field mice (Sacchi et al. 2008; Lopucki et al. 2019).

Low levels of interspecific competition may also be influenced by the early colonization of the urban environment by striped field mice. Pieniazek et al. (2017a) describes the competition that occurs between striped field mice and yellow necked mice (*A. flavicollis*) in Warsaw, Poland. While typically a weaker species, the competitive success in urban environments shifts in favor of striped field mice, possibly due to their tendency to be the first species to colonize cities and longer time to adapt to urban conditions. This phenomenon can be attributed to the priority effect, which describes the impact that a particular species can have on community development by simply being the first species to inhabit an area (Young et al. 2001; Fukami et al. 2005).

Striped field mice are usually nocturnal, but urban individuals are observed to be active during the day in open areas such as parks (Luniak 2004). Instead of organizing their foraging behavior around sunset, when it is dark but temperatures are still warm, Łopucki and Kiersztyn (2019) observed that striped field mice in urban environments of Lublin, Poland, will forage in five distinct peaks during the daytime. These peaks of behavior facilitate long periods of foraging and optimize temperature regulation by avoiding colder night-time temperatures. This change in foraging behavior may be due in part to low rates of predation in urban areas. The most significant predators of the striped field mouse in this region are buzzards (*Buteo buteo*) and least weasels (*Mustela nivalis*) (Łopucki et al. 2019), who are not much of a threat in the city and would ordinarily be present in the daytime. Daytime foraging behavior by field mice might also explain why they experience low predation from owls in urban areas (Gliwicz et al. 1994).

Harms

Gortat et al. (2015) observed that urban striped field mice living in and around the city of Warsaw, Poland, generally show high levels of genetic variance. While migration rates are low, high population densities and the use of green corridors maintain gene flow between patches inhabited by mice. However, gene flow and genetic variability were found to be limited in heavily urbanized areas towards the center of the city, which is thought to be due to isolation caused by ecological barriers and the absence of green corridors in these areas. Low genetic variance and increased relatedness among individuals may result in negative health effects, as genetic disorders are more likely to increase in frequency within isolated, inbred populations (Łopucki & Mróz 2010).

Urban populations of striped field mice in Europe were found to have high levels of parasite infestations (Gliwicz et al. 1994). A study by Dwużnik et al. (2017) found that striped field mice living in city parks in Warsaw showed a high prevalence and abundance of helminth parasites, such as *Heterakis spumosa* and *Heligmosomoides neopolygyrus*. It has been suggested that urban environmental pollution may weaken the immune system of the mice, resulting in a greater susceptibility to infectious agents such as intestinal helminths (Jancova et al. 2006). However, field mice in urban areas exhibit good physical conditions and high population densities (Liro 1985), which may contribute to the efficient transmission and maintenance of parasites (Dwużnik et al. 2017). Parasite infections also vary in their severity, so field mice may be able to carry heavy parasitic loads and remain healthy (Diakou A., pers.comm.; School of Veterinary Medicine, Aristotle University of Thessaloniki, Greece). The extent of harms and sublethal effects caused by parasites on urban field mice remains largely unknown, as most studies have focused on the prevalence and abundance of parasite species, and not their impacts on the health and wellbeing of individual mice.

Passer domesticus (house sparrow)

House sparrows are found in most parts of the world, with large population ranges in North America, South America, Africa, Asia, Europe, and Australia, and are considered to have the largest area of distribution among all wild birds (Fig. 4) (Jernelov 2017; BirdLife International 2021a). As their name suggests, they generally live close to humans, and it is supposed that they have done so since humans began practicing agriculture and husbandry (Jernelov 2017). However, populations of house sparrows have experienced a significant decline in many urban areas of Europe over the last few decades (De Laet & Summers-Smith 2007; De Coster et al. 2015; Bernat-Ponce et al. 2018).

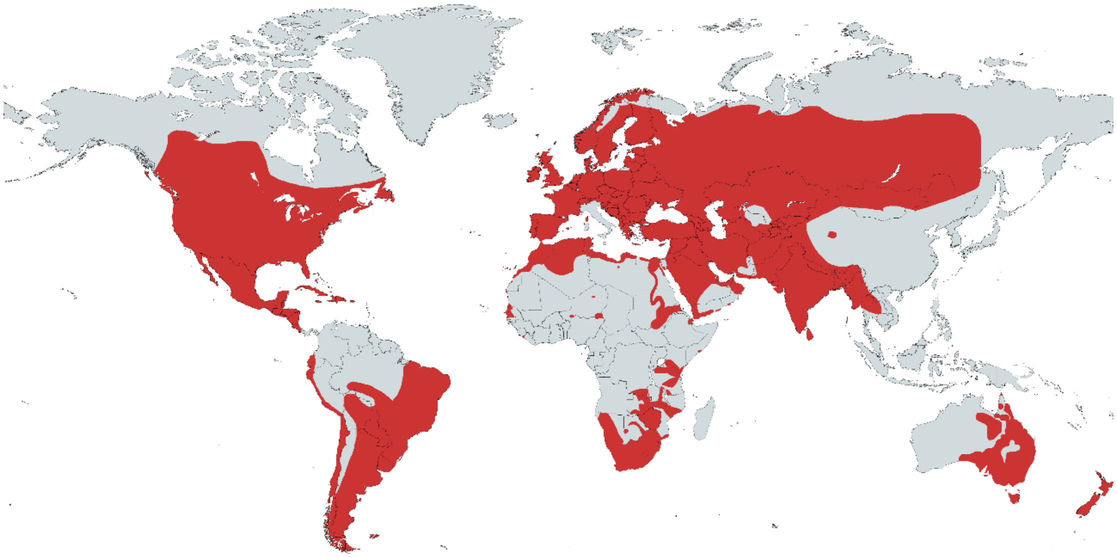

Figure 4. Estimated global distribution of *Passer domesticus (*house sparrow*).* Adapted from BirdLife International (2021a).

Population dynamics

In Britain, populations of house sparrows in suburban gardens have declined by 60% since the early 1970s (Siriwardena et al. 2002). A study by Peach et al. (2008) found that suburban population declines in Leicester, England, may be due to low reproductive success. House sparrow chicks experienced low survival rates and low body masses, which was attributed to multiple factors, including low temperatures, heavy rainfall, high levels of nitrogen dioxide from traffic, and nutritional stress from poor quality diets. The high cleanliness of streets has also been suggested as a contributing factor in declining populations, as this has limited foraging opportunities for house sparrows in urban areas (Siriwardena et al. 2002).

Fernández-Juricic (2001) found that house sparrows in the city of Madrid, Spain, experienced high breeding densities at urban-park edges. This is likely due to their ability to utilize both natural vegetation and nearby buildings for nesting sites, as well their habituation to humans, who provide supplemental food from refuse or deliberate feeding. In southeast Spain, urban house sparrows reached their highest densities in parks and areas where food subsidies were abundant, with lower densities recorded in areas with crowded streets, heavy traffic, and high-rise buildings (Bernat-Ponce et al. 2018). Densities were found to be highest at intermediate levels of pedestrian traffic (Fernández-Juricic et al. 2003), but areas of constant high foot traffic may disturb foraging and breeding activities, positing a limitation to the amount of disturbance that house sparrows can tolerate (Lowry et al. 2012).

Urban house sparrows show a sedentary lifestyle, and their typical home range has a radius of 0.6 to 1.3 miles from the breeding colony (Summers-Smith 1963), although juveniles do disperse from their colony (Siriwardena et al. 2002). They nest in a variety of holes and crevices in buildings, trees, earth-banks, and in the foundations of larger nests, such as those of corvids (Snow & Perrins 1998). House sparrows in the U.K. have shown a preference for nesting in older, less maintained housing (Wotton et al. 2002; Robinson et al. 2005), and it is suggested that a lower degree of home improvements offer more nesting sites within damaged roofing (Chamberlain et al. 2007). In suburban areas of the city of Oxford, England, their presence has been positively correlated with high densities of bushes in front gardens (Wilkinson 2006), which is likely due to their tendency to shelter and forage in bushes (Summers-Smith 1963). Heavily urbanized areas with little to no greenery or are completely devoid of vegetation are mostly avoided by house sparrows (Nath et al. 2019).

Behavior

Risk-taking behavior in house sparrows decreases with predator attacks, which may impact their health and survival as risk-taking behavior is crucial to obtaining food. The older and more experienced that a house sparrow is, the longer their wariness persists after a startle, and the less food is obtained (Seress et al. 2011). The lasting hesitance and anxiety from repeated predator attacks may result in stressed individuals with poor body conditions. Bókony et al. (2010) found that urban house sparrows maintain smaller and leaner bodies for months, even when removed from the urban environment, which suggests that urban individuals may suffer from chronic stress. However, the study also found that the smaller size of the sparrows did not impact their competitive abilities, such as fighting, scrambling, and searching for food.

Skorka et al. (2016) investigated the coexistence of house sparrows with other birds in residential areas of the city of Poznan, Poland. The results found that sparrow abundance was positively correlated with the abundance of pigeons, specifically urban pigeons (*Columba livia*), wood pigeons (*Columba palumbus*), and collared doves (*Streptopelia decaocto*). This suggests that house sparrows may benefit directly from the presence of pigeon flocks as an indicator of scattered food resources, as their diets overlap and sparrows were seen foraging on the ground among pigeons. While some aggressive behaviors between sparrows and pigeons were observed, sparrows fed on smaller food items compared to pigeons, which likely minimized competition for food. The researchers noted that this positive correlation in abundance only occurred in areas where there was a high degree of tall building cover, a favored breeding location for urban pigeons. When the level of tall building cover was low, no association between pigeon and house sparrow abundance was observed.

In Poznan, house sparrow abundance was also affected by the availability of resources. When food resources were low, there was a negative correlation between the abundance of house sparrows and corvids, such as hooded crows (*Corvus cornix*) and magpies (*P. pica*) (Skorka et al. 2016). This may indicate competition among them, as corvids heavily forage on food subsidies (Kristan et al. 2004; Lenda et al. 2012), and may outcompete the smaller house sparrows for limited resources. Skorka et al. (2016) also found that house sparrow abundance was negatively correlated with the abundance of tree sparrows (*Passer montanus*) when resources were low. This negative relationship was also observed when the cover of tall buildings was high, which suggests that there may be competition between the two sparrow species for food and nesting sites. The authors speculate that high numbers of pigeons in tall buildings may indirectly increase competition for nesting sites between house sparrows and tree sparrows.

Kalinoski (1975) observed that house sparrows repeatedly had aggressive encounters with house finches (*Haemorhous mexicanus*) at a bird feeder located in a suburb of Albuquerque, New Mexico. Aggressive behaviors became more frequent as the number of birds present at the feeder increased, and individual feeding space decreased. The highest number of aggressive encounters were observed in winter, when large aggregations of birds gathered at the feeder. The cold weather and snow cover during this period likely resulted in reduced foraging opportunities for birds and a higher dependance on feeders. Shochat et al. (2004) suggest that house finches and house sparrows in urban areas of Phoenix, Arizona co-exist by utilizing different foraging strategies. House sparrows are localized feeders, spending more time at individual food patches, while house finches have larger home ranges and fly long distances, visiting multiple food patches and foraging for shorter lengths of time at each patch. It has also been observed that house sparrows in suburban Montreal avoid confrontation when they can, and will disperse themselves among food patches of lower quality in order to do so (Johnson et al. 2006).

Harms

Herrera-Dueñas et al. (2017) found that urban house sparrows living in the city of Madrid showed higher levels of oxidative stress compared to sparrows living in suburban areas surrounding the city. This is thought to be due to the higher levels of air pollution in the city, as well as a lack of antioxidants in the diet of city-dwelling birds. The effects of oxidative stress may result in tissue damage, reduced survival rates, and shorter lifespans (Isaksson 2015). Oxidative stress may also have a negative impact on the fitness of birds during breeding seasons, when limited antioxidant resources have to be allocated to both self-maintenance and reproduction (Alonso-Alvarez et al. 2004; Herrera-Dueñas et al. 2017). The accumulative effects of reduced fitness in individuals and their offspring may be a contributing factor in population declines of urban house sparrows (Herrera-Dueñas et al. 2017).

In areas of lower socioeconomic status, house sparrow predation is higher due to environmental obstacles they must overcome (Shaw et al. 2008). More specifically, in areas where there are fewer shrubs and green areas, it is harder for house sparrows to evade predators. As a result, there is increased predation from Eurasian sparrowhawks (*Accipiter nisus*), domestic cats (*F. catus*), and tawny owls (*Strix aluco*), the last of which are more likely to prey upon house sparrows instead of mice in urban environments (Goszczynski et al. 1993). There have been conflicting studies regarding the relationship between Eurasian sparrowhawks and adult house sparrow abundance (Bell et al. 2010; Peach et al. 2018), but no temporal trends in sparrow abundance and hawk activity. Predators in urban environments not only pose an immediate risk to adult sparrows, but the increasing effort required to evade these predators also impacts the ability of the adults to care for juveniles, negatively impacting their survival as well (Baker et. al. 2005).

Several studies have shown that urban house sparrows have small body sizes and low body masses (Liker et al. 2008; Seress et al. 2011; Meillère et al. 2015). While nutritional deficiency might be an obvious suggestion, the consistent abundance of food available in urban environments shows otherwise. Other physical characteristics, such as wing length and muscle mass, indicate that urban adult house sparrows are not suffering from nutritional stress (Seress et al. 2011; Meillère et al. 2015). However, juvenile house sparrows in urban environments have been found to have high fat stores, indicating they may be ingesting food subsidies with high fat content in their diets (Meillère et al. 2015). This may have a negative effect on their growth and development, as these kinds of foods may not meet the nutritional requirements of young house sparrows (Anderson 2006; Chamberlain et al. 2009; Meillère et al. 2015). An analysis of feathers from juvenile house sparrows in France revealed that levels of the stress hormone corticosterone were higher as the level of urbanization increased, suggesting that chicks suffer from stressful conditions during development in urban environments, which may be attributed to poor-quality diets (Beaugeard et al. 2018).

Avian malaria is another pressure impacting urban house sparrows and their survival. Dadam et al. (2019) found that 74% of house sparrows living in suburban areas of London have been infected by the parasite *Plasmodium relictum*, one of several parasites that cause avian malaria, and in some colonies 100% of the birds were infected. The intensity of *P. relictum* infections were found to be negatively associated with winter survival rates of juvenile and adult sparrows, as well as the growth rate of the populations. Juvenile birds suffered from greater intensities of infections compared to adults, which may be contributing to population declines due to lower survival and recruitment of juveniles (Peach et al. 2015). Dadam et al (2019) note that the impact of house sparrow infections may have been underestimated in their study, as sparrows suffering from intense parasite infections may have died before they could be tested. Infected birds may suffer from symptoms including lethargy, ruffled feathers, anemia, loss of appetite, diarrhea, and death in cases of heavy infections (Atkinson 2008). It is unclear whether the birds die from avian malaria, or if the disease prevents them from performing behavior vital to survival, such as foraging and evading predators.

West Nile virus is another illness predominantly found in house sparrows. Like malaria, the virus is transmitted by mosquitoes, but primarily affects the central nervous system. Birds that have been infected with West Nile virus experience loss of coordination, head tilt, tremors, weakness, and apparent blindness (Cornell Wildlife Health Lab (CWHL) 2018b). House sparrows are considered to be prominent carriers and amplifiers of the disease, as the virus is spread rapidly through the abundance of infected sparrows. Kernbach et al. (2019) found that urban house sparrows maintain higher burdens of this virus due to artificial light. Excess light interrupts immune responses, causing the birds to remain infectious for 2 more days than they otherwise would. The result is that the virus is 41% more likely to cause an outbreak, increasing the probability of infection for many more birds.

The most common ectoparasites that occur on house sparrows are mites, ticks, and feather lice, which can negatively impact the health of birds when they occur in heavy loads (Anderson 2006). Urban house sparrow chicks from broods with high nest mite loads were found to have lower body masses (Weddle 2000), which may negatively affect their chances of survival (Ringsby et al. 1998). Galbraith et al. (2017) found that house sparrows who visited feeding stations in urban areas of New Zealand had heavier loads of feather lice compared to sparrows from areas where no feeders were present. Increased rates of lice transmission were thought to be facilitated by high densities of sparrows at feeders. When extensive, feather lice infestations can cause damage to plumage, as well as impacting thermoregulation, fitness, and survival (Bush & Malenke 2008).

Columba livia (urban pigeon)

Urban pigeons, also known as street pigeons, city pigeons, and house pigeons, are descended from rock pigeons, also called rock doves (Johnston & Janiga 1995). Although they exhibit differences in traits from their rock pigeon ancestors, urban pigeons are not considered to be a distinct subspecies, and are instead classified as a variety or breed of rock pigeon, capable of interbreeding with other varieties of pigeons (Johnston & Janiga 1995; Stringham et al. 2012). Populations of urban pigeons are found throughout the world, in cities and towns of Europe, North America, South America, Africa, Asia, and Australia (Fig. 5) (Lever 2010).

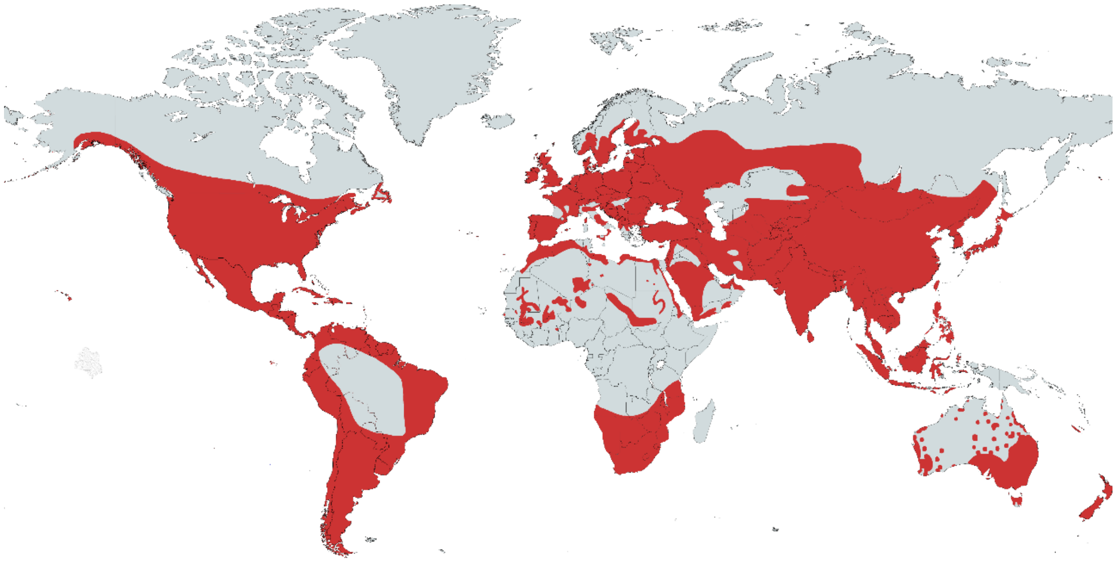

Figure 5. Estimated global distribution of *Columba livia* (urban pigeon). Adapted from Gibbs et al. (2001) and BirdLife International (2021b).

Population dynamics

The success of urban pigeons in urban environments is a result of multiple factors, including the lack or low levels of predation (Sol et al. 1998), the lack of cold and stress in winter due to urban heat island effects (Dobeic et al. 2011), the ease of finding resources during winter (Jokimaki & Suhonen 1998), and the high protein content of food subsidies (Ciminari et al. 2005). Urban pigeons also benefit from the abundance of nesting, perching, and roosting spaces in urban infrastructure, such as building ledges, overhangs, and bridges (Savard & Falls 1981; Hetmański et al. 2011; Przybylska et al. 2012; Sacchi et al. 2002; Ali et al. 2013; Pike et al. 2016). It is thought that these spaces provide refuges that are similar to the caves and ledges of rock cliffs, which were utilized by their rock pigeon ancestors (Johnston & Janiga 1995; Larson et al. 2005).

When food is abundant and weather conditions are favorable, urban pigeons are capable of breeding throughout the year, with the majority of reproduction occurring in late spring and summer (Dunmore & Davis 1963; Murton et al 1972; Johnston & Janiga 1995; Hetmański & Wołk 2005; le Roux et al. 2013). Clutches typically consist of two eggs, and clutch size appears to be limited by the energetic costs of the parents during the early stages of nestling development (Burley 1980; Johnston & Janiga 1995). However, breeding pairs are capable of caring for two clutches at the same time (Burley 1980). When the young from the first clutch reach the stage where they require less parental care, females may lay a new clutch of eggs and begin incubation, allowing them to increase the number of clutches in a breeding season (Johnson & Johnston 1989; Hetmański & Wołk 2005). Nestling mortalities and egg losses may occur due to falling from nests, illness, lack of food due to competition from other juvenile birds, and predation. (Hetmański & Barkowska 2007; le Roux et al. 2013). Juveniles disperse only marginally and young birds who leave their natal colonies usually relocate to colonies with a lower density of breeding pairs (Hetmański 2007).

Population densities of urban pigeons tend to increase as they get closer to the center of cities (Johnston & Janiga 1995; Jokimaki & Suhonen 1998; Sacchi et al. 2002; Clergeau et al. 2006; Ferman et al. 2010; Przybylska et al. 2012), although these densities may fluctuate seasonally (Ryan 2011; Ali et al. 2013) and inter-annually (Amoruso et al. 2014). Urban densities are related to food availability, including intentional feeding, discarded food, and waste (Buijs & Van Wijnen 2001; Morand-Ferron et al. 2009), which is also associated with human population density (Hetmański et al. 2011). Predation rates tend to be smaller in city centers compared to city edges and suburbs, which may also contribute to higher numbers of pigeons (Gering & Blair 1999; Sorace & Gustin 2009; Przybylska et al. 2012). The availability of roosting and nesting sites is also likely to affect pigeon densities (Johnston & Janiga 1995). The highest densities of urban pigeons living in cities of Italy and Pakistan were found in older buildings made with bricks and roof tiles, which provide more openings and opportunities for nest sites compared to newer buildings in these areas, which are made with glass and concrete (Sacchi et al. 2002; Ali et al. 2013). In the city of Poznan, Poland, urban pigeon densities were highest in areas with a high percentage of tall building cover (Przybylska et al. 2012).

Behavior

Pigeons in urban environments tend to forage in flocks, and visit many foraging sites each day (Lefebvre 1985; Gibbs et al. 2001). Urban pigeons also show individual foraging strategies, with some pigeons foraging close to their roosting sites, while others may fly many miles to surrounding areas to find suitable foraging sites (Johnston & Janiga 1995). Different foraging strategies may represent a trade-off in energetic costs and predation risk, as foraging closer to roosting sites requires less energy and carries a low risk of predation, but less reliable food sources (Rose et al. 2006). In the city of Basel, Switzerland, Rose et al. (2006) found that female pigeons flew significantly longer distances than males from their roosting sites to visit foraging sites in agricultural areas surrounding the city. This may be due to female pigeons preferring to fly further distances to gain access to more abundant and reliable food sources (Johnston & Janiga 1995), and avoiding competition with males at smaller, more concentrated food sources (Haag 1984, in Rose et al. 2006). Females also require more energy for reproduction, and energy costs during the egg-laying period may be 15-85% higher compared to males (Walsberg 1983). Egg production may decline as a result of reduced food consumption (King 1973), so females may invest more energy in accessing abundant food sources to meet reproductive requirements.

Urban pigeons show a high degree of tolerance for humans, and will often congregate in areas of high human activity, such as cafes, park entrances, grocery stores, and fast-food restaurants, where people are likely to drop or offer food (Goodwin 1960; Przybylska et al. 2012). In Montreal, urban pigeons were found to visit a number of possible foraging sites at different times of the day, and appeared to have learned through experience to monitor sites where food availability varied (Lefebvre & Giraldeau 1984). During the COVID-19 pandemic of 2020 in Singapore, Soh et al. (2021) observed there was a significant increase in the number of urban pigeons foraging in green spaces, such as parks, and a decline in the number of pigeons foraging in areas of typically abundant food subsidies, such as open food centers. This is believed to be caused by the decrease in human activity and human provided food during the pandemic lockdown, and demonstrates that urban pigeons are able to adjust their foraging behavior in response to changes in food availability.

Goodwin (1960) observed that urban pigeons in London will sometimes compete with wood pigeons (*Columba palumbus*) for human-provisioned food. The author noted that aggressive behavior between the two species only occurred when they attempted to use the same perching space to gain food, such as window ledges or human hands. On window ledges, urban pigeons were able to dislodge wood pigeons more often, as they are well adapted to utilizing these perching sites. However, wood pigeons are able to swallow larger pieces of food, and will sometimes take food from the mouth of an urban pigeon who is attempting to swallow a large food item. Goodwin (1960) notes that other food competitors for urban pigeons in London include black-headed gulls (*Larus ridibundus*), mallards (*Anas platyrhynchos*), and house sparrows (*P. domesticus*), especially during winter. Black headed gulls appear to be the most aggressive competitors, often pushing and pecking their way into a flock of foraging pigeons, and consuming large amounts of food very quickly. House sparrows are smaller than pigeons, and are unable to push into pigeon flocks, but can quickly fly into openings and carry away food items. Skorka et al. (2016) suggested that competition between urban pigeons and house sparrows is reduced by house sparrows feeding on smaller items.

Harms

Although rock doves are granivores, urban pigeons may also eat small invertebrates, insects, and human food (Lefebvre & Giraldeau 1984, Jokimaki & Suhonen 1998). In some urban locations, they rely heavily on food subsidies, with bread and cake making up the majority of the diet of urban pigeons living in the city of Leeds (Murton & Westwood 1966), and populations in London have also been observed eating mainly discarded or provisioned food, such as bread (Goodwin 1960; Palmer 2003). This type of diet has been found to cause higher levels of acidity in their excreta (Spennemann & Watson 2017), and the lack of essential nutrients may result in illness, reduced immunity strength (Dobeic et al. 2011), and a higher susceptibility to parasite infestations (Schreiber et al. 2015). Pigeons may also compensate for low-quality diets by increasing their food intake (Spennemann & Watson 2017).

Urban pigeons often exhibit signs of leg injuries, foot deformities, and missing toes, which have been attributed to materials such as string or human hair becoming entangled in the pigeons' feet, where it can tighten and cut off blood circulation (Skandrani et al. 2018; Jiguet et al. 2019). This problem is known as stringfoot, and can result in infection, tissue death, and loss of toes and feet (Jiguet et al. 2019; Palomacy 2020). Although they can recover and survive with these injuries (Palomacy 2020), stringfoot can cause high levels of stress and pain in affected pigeons, and may negatively impact their mobility, balance, and abilities to forage and avoid predators (BirdSpot 2021). Their ability to groom themselves may also be affected, which can increase their susceptibility to parasite infections, and reduce the reproductive success of male pigeons, as they become less attractive to females (Clayton 1990; Naish 2014; BirdSpot 2021). Pigeons typically use twigs, straw, leaves, and hay to build their nests, but in urban areas, they will also use string, twine, and human hair for nesting, which can become tangled around the limbs and necks of young birds, and may result in injuries, loss of limbs, or death (Palomacy 2020).

The number of foot mutilations in urban pigeons has been correlated with the density of people living in the area, as well as the cleanliness of the ground (Skandrani et al. 2018). Jiguet et al. (2019) studied flocks of pigeons from 46 different sites within the city of Paris, and found that the number of mutilated or injured toes in urban pigeons was higher in city blocks where a greater number of people lived, and lower in areas with a greater density of green urban spaces. This is most likely due to the increased likelihood of pigeons encountering hair or string on the ground where human activity is higher. A higher number of hairdressers in an area also correlated with a higher number of pigeon foot mutilations, which could possibly be due to more human hair strands ending up on sidewalks and pavements from residual hair cuttings. However, this may also be an indirect effect of human population density, as more hairdressers are found in areas of higher human density.

Pteropus alecto (black flying fox)

Black flying foxes, also called black fruit bats, belong to one of 65 species of large flying foxes of the genus *Pteropus* (Hall & Richards 2000). Black flying foxes occur in Australia, Papua New Guinea, and Indonesia (Fig. 6), and are typically found along coastal areas

(Hall & Richards 2000; Roberts et al. 2017). Individual black flying foxes tracked by satellite transmitters have been observed traveling hundreds of miles over land and sea, moving between the north of Australia, Papua New Guinea, and Indonesia, utilizing savannah, mangrove, forest, riparian, and urban environments (Breed et al. 2010). In Australia, flying foxes have become increasingly abundant in urban areas over the last 25 years (Kung et al. 2015), with many camps of black flying foxes becoming established in cities and towns along the coasts of Queensland and New South Wales (NSW) (Plowright et al. 2011; Australian Government, Department of Agriculture, Water and the Environment (ADAWE) 2019).

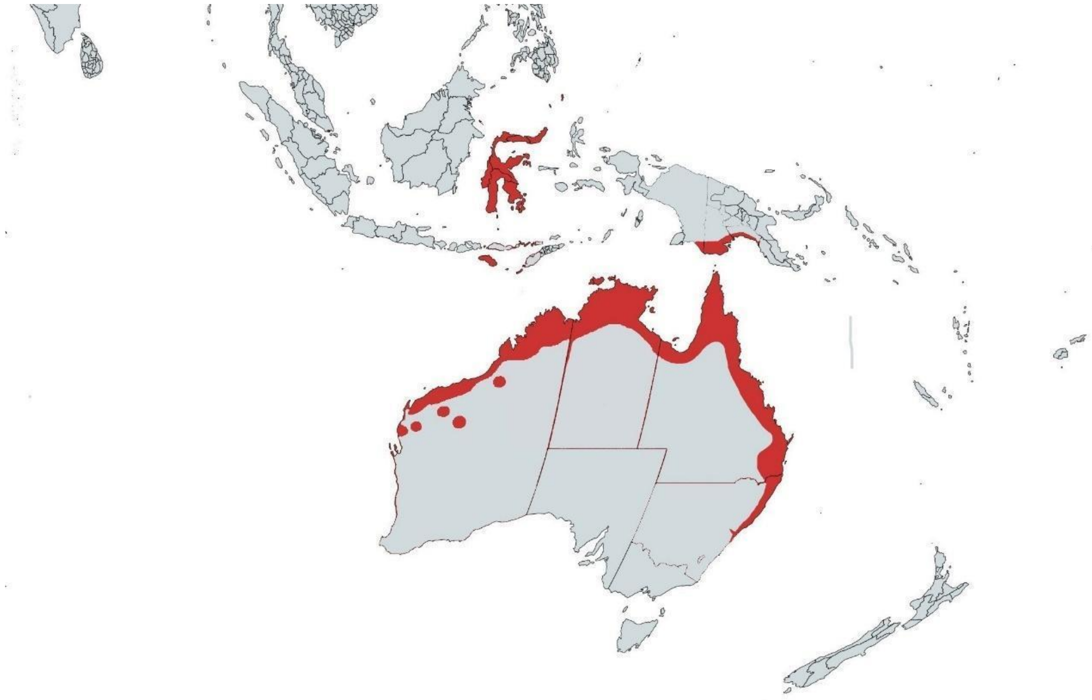

Figure 6. Estimated global distribution of *Pteropus alecto* (black flying fox). Adapted from IUCN (2017).

Population dynamics

While there has been little research investigating survival and reproduction black flying foxes, there seem to be similar patterns among different *Pteropus* species based on the information that is available (Pierson & Rainey 1992). Bats from the *Pteropus* genus, including the black flying fox, exhibit a slow life strategy, and take at least 18 months to mature, which is indicative of long lifespans (Pierson & Rainey 1992; Queensland Government, Department of Environment and Science (QDES) 2011). Females start to breed at 2 to 3 years of age, typically giving birth to only one offspring per year, with gestation lengths ranging from 140 to 192 days, and juveniles may be dependent on their mothers for up to a year (Falanruw 1981; QDES 2011). Based on these reproductive patterns, the population growth rates for *Pteropus* species are low relative to other mammals of similar size (Pierson & Rainey 1992).

Like all *Pteropus* species, black flying foxes are primarily herbivores, mostly feeding on fruits and flowers (QDES 2011; Griffith et al. 2020). Black flying foxes will feed on a variety of plants, and are likely attracted to urban environments due to the high availability of different plants throughout the year (Plowright et al. 2011; Páez et al. 2018). This high abundance of food has resulted in limited migratory behavior in many urban flying fox populations (Plowright et al. 2011). The duration of time spent at an urban food patch is influenced by several factors, including the initial density of food within a patch, the rate at which food is consumed, and the degree of patch isolation (Páez et al. 2018). The timing of flying fox births is dependent on food availability, as most young are born around periods of high plant productivity when food is abundant (Vardon & Tidemann 1998).

Fluctuating population densities of black flying foxes are also influenced by food availability, with camps forming at times of high food abundance and dispersing when plant productivity is low (Nelson 1965b, in Pierson & Rainey 1992; Palmer et al. 2000; Birt 2004). Flying fox camps in Australia appear to reach their largest sizes during November and December (Pierson & Rainey 1992). Population ranges of black flying foxes in Australia have extended further south during the last century, which is also thought to be driven by their diet (McWilliam 1986, in Griffith et al. 2020). An estimated 170, 000 black flying foxes were surveyed in eastern Australia in 2019 (Commonwealth Scientific and Industrial Research Organisation (CSIRO) 2019), with population sizes of urban camps ranging from hundreds to thousands of individuals (ADAWE 2019). Little is known about the size of populations in other regions (Roberts et al. 2017).

Behavior

Flying foxes roost together in camps during the day and forage at night, sometimes traveling over 30 miles from their camp in search of food (Currey et al. 2018). Camps are where social behaviors and interactions most frequently occur, such as birthing, rearing, courtship, and mating (Markus & Blackshaw 2002; Currey et al. 2018). Markus and Blackshaw (2002) studied suburban populations of black flying foxes in Brisbane, Queensland, and observed them roosting in trees during the day to sleep, groom, and rest, with individuals spaced about 12 inches apart. Individuals were sometimes seen defending their personal roosting space when settling in to camps at dawn, but this behavior was usually limited to aggressive vocalizations. Male flying foxes sometimes defended courtship territories from other males during mating seasons, but no injuries were observed, as territorial behaviors mostly consisted of vocalizations and chasing away intruders, and only occasionally involved physical contact (Markus 2002; Markus & Blackshaw 2002).

Black flying foxes occur in sympatry (occupying the same areas) with grey-headed flying foxes (*Pteropus poliocephalus*) in NSW, Australia. It has previously been thought that these two species compete for food resources, but a study of populations in urban park forest fragments suggests that they partition resources, with grey-headed flying foxes preferring pollen, and black flying foxes preferring fruit (Griffith et al. 2020). Suburban populations of black and grey-headed flying foxes in Brisbane were observed occupying the same camp, and were often seen roosting in the same trees and branches without any evidence of aggressive behavior between the two species (Markus 2002).

There has been limited research conducted regarding vigilant behavior in urban black flying foxes. Observations of Brisbane suburban populations by Markus and Blackshaw (2002) showed that individuals rarely moved from their roosting positions during the day, unless they were disturbed by noise or sudden activity nearby. In response to perceived threats, such as large crows or humans, individuals at the edge of the camps would sometimes sound a shrill alarm call, often resulting in other camp members climbing or flying away from the direction of the perceived threat. Usual roosting behavior resumed 10 to 20 minutes after the perceived threat or disturbance ended. It is unknown if black flying foxes increase or decrease their vigilance in urban environments, or if there are any costs associated with this behavior, such as higher energy expenditure or less time spent foraging.

Harms

Flying foxes are particularly vulnerable to extreme heat events, as their roosting sites are in the branches of canopy trees during the day, where they may be partially exposed to the sun (Welbergen et al. 2008; NSW Department of Planning, Industry and Environment (NSW DPIE 2020). Once temperatures exceed 95°F, flying foxes will attempt to reduce their body temperature by seeking shade, fanning themselves with their wings, panting, licking their wrists and wings, and descending to lower branches or to the ground, but these strategies cease being effective in extremely high temperatures (Welbergen et al. 2008; Stanvic et al. 2013; NSW DPIE 2020). Flying foxes suffering from heat stress, or hyperthermia, may become dehydrated, lethargic, fall from trees, and can die when temperatures exceed 107°F (Welbergen et al. 2008; NSW DPIE 2020; Lab of Animal Ecology 2021). Since 1994, at least 35 extreme heat events in Australia have resulted in mass deaths of flying foxes, cumulatively killing over 160,000 individuals, with many from camps in urban areas including Melbourne, Sydney, and Townsville (Welbergen et al. 2008; Lab of Animal Ecology 2021).

A study by Welbergen et al. (2008) investigated the deaths of thousands of flying foxes who were killed by extreme heat on January 12th, 2002 when temperatures reached over 107°F. At least 7 of the affected camps were located in urban areas of NSW, and were inhabited by both black and grey-headed flying foxes. Black flying foxes suffered much higher rates of mortality than grey-headed individuals, indicating that black flying foxes may be more susceptible to extreme temperatures than other *Pteropus* species. Higher mortalities were recorded in young flying foxes and adult females compared to adult males, which is likely to have long term effects on reproduction rates and population sizes. Another heatwave on January 4th, 2014 in southeast Queensland killed more than 45,500 flying foxes in one day, 96% of which were black flying foxes, and many from urban camps (Welbergen et al. 2014). These numbers are thought to be conservative estimates, since many deaths go unnoticed or unrecorded (Welbergen et al. 2008; Welbergen et al. 2014). Increasingly warm temperatures over the last few decades mean that extreme heat events such as these are likely to escalate in the future (Lab of Animal Ecology 2021).

Flying foxes are hosts of the Hendra virus (HeV), a zoonotic virus that can cause potentially fatal respiratory and neurological diseases in humans and horses (Hall & Richards 2000; Halpin et al. 2011). While it is not fatal to flying foxes, and they rarely show any signs of disease when infected (Halpin et al. 2000; Rural Industries Research and Development Corporation (RIRDC) 2016), the high prevalence of HeV found in a population of nutritionally stressed flying foxes indicates that their immune response to the virus may carry high energetic costs (Plowright et al. 2008). HeV has been detected predominantly in black flying foxes and spectacled flying foxes (*Pteropus conspicillatus*), and is detected much less often in other Australian *Pteropus* species (RIRDC 2016). Flying foxes in southern Queensland and northern NSW show the highest prevalence of the virus, and detection rates are higher during winter (RIRDC 2016).

As they are able to travel long distances and often share foraging and roosting sites, infected flying foxes have the potential to spread HeV to other flying fox populations (Halpin et al. 2000; Breed et al. 2010). Plowright et al. (2011) used a spatial model to examine patterns of HeV transmission in black and grey-headed flying fox populations. The simulated effects of decreased migratory behavior and greater aggregation in urban flying foxes showed that there is the potential for outbreaks of the virus to become larger and more intense, but less frequent, in urban populations. More specifically, decreased connectivity between populations enhances epidemic size by increasing the duration of time between viral introductions. This allows subpopulations to recruit more susceptible individuals in the absence of infection, resulting in the loss of herd immunity.

HeV is excreted by flying foxes via urine and birth fluids, and it is thought that the virus can potentially be transmitted to horses who come in contact with these excreted fluids (Halpin et al. 2000; Plowright et al. 2008). However, the opportunity for transmission is limited by the amount of virus that is excreted, and the short time that the virus is able to survive in the environment outside of a host, therefore more research is needed to determine other possible factors involved in HeV transmission to horses (Halpin et al. 2011; RIRDC 2016). There is no evidence of flying foxes infecting humans with HeV (Hall & Richards 2000; Kung et al. 2015; RIRDC 2016), but many people mistakenly believe that they can contract the virus from direct contact with flying foxes, which has contributed to negative attitudes towards them from the public, in the media, and from policy-makers (Degeling & Kerridge 2013; Kung et al. 2015; RIRDC 2016).

Iguana iguana (green iguana)

Green iguanas are a large tree-dwelling species of lizard belonging to one of eight genera in the family Iguanidae (Buckley et al. 2016). They are also called common green iguanas, and are known as American iguanas in Fiji, to distinguish them from the green Fijian iguana species (Harlow and Thomas 2010, in Falcón et al. 2013; Buckley et al. 2016). Juveniles are typically bright green, but the color of adult green iguanas can range from bright green to dark greenish- brown or gray, with markings of various color patterns (Falcón et al. 2013). Green iguanas have a wide distribution through South America, and populations are also found in North America, and the Caribbean and Pacific Islands (Fig. 7) (Buckley et al. 2016; Bock et al. 2020 [2018]). In the last few decades, there have been reports of green iguanas becoming increasingly abundant in urban areas (Townsend et al. 2003). This is thought to be largely due to the popularity of green iguanas as pets, particularly in Florida, where they sometimes escape or are intentionally released by owners who find them difficult to care for (Townsend et al. 2003; Meshaka et al. 2004; Krysko et al. 2007).

Figure 7. Estimated global distribution of *Iguana iguana* (green iguana). Adapted from IUCN (2016).

Population dynamics

Populations of green iguanas occur in urban areas of southern mainland Florida and the Florida Keys (Meshaka et al. 2004), and it is thought that colder winter temperatures have limited their range and expansion further north (Townsend et al. 2003). It has been suggested that the numerous canal systems in Florida have facilitated the dispersal and colonization of iguanas in new areas (Meshaka et al. 2004; Krysko et al. 2007). Populations have also been reported in cities and towns of Pueto Rico (García-Quijano et al. 2011; Gomez et al. 2020), and in urban areas of Trinidad and Tobago (Auguste 2020). They almost always occur near bodies of water, and prefer areas with trees over water and abundant edible vegetation (Meshaka et al. 2004). In urban environments, they are typically found in areas with plenty of foliage, low numbers of potential predators (Campbell 2011), and nearby bodies of water such as bays, estuaries, canals, channels, ponds, and ditches (Meshaka et al. 2004; García-Quijano et al. 2011). In areas with little or no trees, such as vacant lots and cleared canal banks, they may also seek shelter in drainage pipes, culverts, burrows, and piles of rock or debris (Krysko et al. 2007). Green iguanas have been observed basking in many different urban and suburban areas, such as residential lawns, pavements, roads, park benches, airport runways, and golf courses (Townsend et al. 2003; Krysko et al. 2007; Gomez et al. 2020).

Females tend to migrate to nest and lay their eggs in sandy beaches near water (Montgomery et al. 1973). In the Florida Keys, nesting areas are limited due to large limestone formations beneath the surface, and females will sometimes use landscaping soil and mulch piles for nesting sites (Krysko et al. 2007). Annual breeding seasons are associated with rainfall patterns, with nesting beginning when it's dry, and hatchlings emerging at the beginning of rainfall and new vegetation (Bock & Rand 1989). The age at which female green iguanas begin nesting varies anywhere from 2 to 8 years of age, with the first nesting of most females occurring when they are 4 or older (Rand & Zug 1987; Bock et al. 2016). This high variance in age is different from most reptile species, who typically begin reproducing around the time they reach a certain size or age, and suggests that environmental factors may influence the time that female green iguanas begin to reproduce (Bock et al. 2016). As there has been little research regarding this, the degree to which urban environmental factors may influence green iguana reproduction is unknown, but likely factors include the availability of suitable nesting sites, abundance and quality of edible vegetation, and environmental temperatures.

High densities of green iguanas have been reported in green spaces, such as botanical gardens and parks, within urban areas of Florida (Meshaka et al. 2004; Smith et al. 2007; Campbell 2011), with the highest densities recorded along the coast (Meshaka et al. 2004). There are relatively few predators and food competitors for iguanas in urban and suburban southern Florida, which may account for the very high densities in these areas (Townsend et al. 2003; Meshaka et al. 2004). López-Torres et al. (2012) also suggested that low levels of predation and competition may have contributed to high population densities in urbanized areas of Puerto Rico.

Behavior

During mating seasons, male iguanas will establish mating territories, usually in areas where there are high densities of females (Rodda 1992). Smaller males can become displaced by larger males, and may alter their movements to avoid entering larger male territories (Rodda 1992; Falcón et al. 2013). Males will display territorial behaviors, such as posturing and patrolling to advertise their territory to females, and to intercept any male intruders (Rodda 1992; Campbell 2011). When another male enters his territory, a territorial male will start bobbing his head and slowly approaching, and may become aggressive if the intruding male does not retreat (Rodda 1992; Pianka & Vitt 2003; Krysko et al. 2007). High population densities in urban areas are likely to affect these breeding behaviors, as there are more males to compete with.

Aggressive territorial interactions can sometimes result in wounds and injuries that may have long lasting effects (Pianka & Vitt 2003). Rodda (1992) observed aggressive interactions between male green iguanas in Venezuela that involved wrestling and biting, and while most lasted less than 30 seconds, one pair of males were observed fighting for 45 minutes. Another male iguana had lost the use of several of his foreclaws, which was thought to be due to a combative injury, and had a hindered ability to climb trees and defend his territory. The following year he was still unable to use several of his foreclaws, and although he attempted to establish his own territory, he was unable to attract any females, and after a few days his territory was abandoned. These kinds of injuries are also likely to negatively impact an iguana’s ability to forage in trees and avoid predators. The number of aggressive male interactions may increase in areas where population densities are high (Brattstrom 1974), but to date there have been no studies investigating this in urban green iguana populations.

When confronted with a threat, green iguanas may flee and seek refuge in a nearby tree, dive or drop from a tree into water, or stand in a defensive posture and use their tails to defend themselves (Rivas & Levin 2004; Falcón et al. 2013). Iguanas may also freeze in place to avoid detection, and their coloration helps to camouflage them amongst vegetation, making them inconspicuous to potential predators (Swanson 1950; Rivas & Levin 2004). In an urban population of green iguanas in West Palm Beach, Florida, Campbell (2011) noted that females and juveniles generally avoided people, and fled if approached, while males were more tolerant of humans, often allowing them to approach within a few feet. Rivas and Levin (2004) also observed that female green iguanas tended to freeze, hide, or flee from potential predators, while males engaged in more risk-taking behaviors, such as running in front of a threat, and climbing onto a female to cover her. The authors speculated that this risk-taking behavior may be altruistic, as drawing attention to themselves provides an opportunity for other iguanas to escape or avoid detection. Living in high densities may be advantageous for urban iguanas, as individuals can observe predator avoidance reactions of their neighbors, and gain early warnings of potential threats (Rodda 1992).

Harms

Although they are herbivores, primarily eating leaves from trees, green iguanas are also opportunists, and may eat other types of food under stressful conditions, or if there is a low supply of their preferred plants (Barten 2006; Britton 2002 [1996]; Govender et al. 2012). This is likely in urban areas where there is typically a high availability of food subsidies, and less vegetation. As their digestive system is adapted to digest plants, animal protein can be particularly harmful to iguanas, and in large amounts, may cause gout, dehydration, metabolic bone disease, renal failure, kidney stones, and death (Britton 2002 [1996]). An excess of fiber in their diet can also be harmful, and may negatively affect an iguana's growth rate, digestion, and metabolism (Baer et al. 1997).

Cold weather conditions have significant effects on green iguanas, as they are ectotherms, who rely on environmental temperatures to regulate their body temperature

(Tosini & Menaker 1995). Once temperatures start to drop below about 10°C/50°F, they become lethargic, cold-stunned, and immobile as their blood pressure and metabolic rate slows down, and prolonged exposure to the cold can be fatal (Krysko et al. 2007; Campbell 2011; Gibbens 2018). Iguanas may seek shelter in burrows, in bodies of water, and under buildings to escape the cold (Townsend et al. 2003; Campbell 2011), and can raise their body temperature by basking in the sun, but they are unable to do this at night or in overcast weather conditions (Krysko et al. 2007; Campbell 2011). During periods of cold weather in Florida, there have been numerous reports of cold-stunned green iguanas falling from trees and lying immobile on the ground in urban areas (Goldenberg 2010; Kobilinsky 2018; Torres 2020). Although they are able to recover once temperatures begin to warm again (Gibbens 2018), there are risks of injuries or mortality when they fall. They are also extremely vulnerable in their cold-stunned state as they are unable to move, and may experience weakened body conditions, gastrointestinal problems, and anorexia after a cold-stun event (Barten 2006; Campbell 2011).

In January 2010, south Florida experienced a period of extreme cold weather, with temperatures in West Palm Beach recorded at 45°F or below for 12 consecutive days (National Oceanic and Atmospheric Administration (NOAA) 2010). Following the extreme cold event, Campbell (2011) found that there were significant declines in two urban populations of green iguanas in the area. Many individuals died during the cold weather period, and while others recovered, their health was negatively impacted by hypothermia and a lack of food while in their cold-stunned state. Juveniles and adult females were the most affected, and there was a decrease in territoriality and breeding behaviors for several months after the cold weather event, with no nesting behaviors or hatchlings observed the following summer. This was thought to be due to decreased fitness at the start of the breeding season, which is likely to have long-term impacts on the iguana populations.

Helping urban wild animals

The welfare of wild animals is impacted by a range of different harms in urban environments, but there are ways we can help to reduce their suffering. The design, construction, and management of urban areas should be conducted with the consideration of their impact on wild animals. Implementing features such as wild animal corridors, overpasses, and other passages can enhance the ability of animals to safely move through urban environments (Fernández-Juricic 2000; Palmer 2003; Snep et al. 2003; Adams et al. 2005). Establishing regular cleaning routines of urban streets and sidewalks may reduce cases of stringfoot injuries in urban pigeons, particularly in areas of high human activity, as the number of foot mutilations have been found to increase in areas with higher densities of humans (Jiguet et al. 2019). Artificial refuges such as nest boxes and burrows can provide shelter and nesting sites for urban animals, and offer some protection against extreme weather events. However, refuges should be trialled and monitored to ensure they meet the needs of the urban animals they are intended for, and to identify any possible detrimental effects they may have on individual animals (Cowan et al. 2021). In urban flying fox camps, the shade provided by layered ground, understory, and canopy cover can reduce the risk of heat stress and dehydration when temperatures are high (Stanvic et al. 2013; Parry-Jones 2018).

Resources can be provided to assist urban animals during extreme weather events, such as additional water sources during heatwaves. Several intervention methods have been developed to reduce the severity of extreme heat events in flying fox camps. Heat-stressed flying foxes can be manually sprayed with water using hoses or hand-held sprayers, which has shown to be effective, as flying foxes often respond by becoming more alert, licking the water, and climbing higher into the tree canopy (Stanvic et al. 2013; Parry-Jones 2018). Alternatively, water can be sprayed in a fine mist into camps from hoses or canopy-mounted sprinkler systems to cool and hydrate flying foxes, as direct spraying and the increased presence of humans may elevate stress levels in some individuals (Department of Environment and Climate Change NSW (DECCNSW) 2008; Parry-Jones 2018; Mo & Roache 2020). Ground-based sprinklers have also been used to cool camps and provide pools of water for flying foxes to drink from (Parry-Jones 2018). However, the noise and motion of sprinklers may disturb flying foxes, and increased humidity may intensify heat stress under certain conditions, therefore more research and trials are required to determine which cooling methods are the most effective in urban camps (Parry-Jones 2018; Mo & Roache 2020).

During periods of cold weather and heavy storms, nesting boxes and artificial shelters can provide warmth and refuge for urban animals. Although artificial shelters can provide some protection against the cold for reptiles, they are unlikely to provide enough warmth to prevent cold-stunning once temperatures drop below 10°C/50°F, but may provide some protection from additional harms once they enter a cold-stunned state. Cold-stunned turtles are often admitted to animal rescue and rehabilitation centers, where they are slowly warmed up and evaluated for injuries or health issues (Turtle Hospital 2014; Turtle Island Restoration Network 2018). Similar facilities or warming centers could be provided for urban iguanas during periods of cold weather, providing them a safe place to warm up and recover from cold-stunning events.

Vaccinations against harmful diseases can increase survival and reduce suffering in many urban wild animals. The administration of the oral rabies vaccine has been very successful in protecting many urban animals from the disease, including racoons, skunks, foxes, and coyotes (Rosatte et al. 1990; Abbott 2020; Müller & Freuling 2020). While several experimental and commercial vaccines against West Nile Virus (WNV) in wild birds have been developed and evaluated, with some resulting in reduced disease and mortality associated with WNV, none have yet been approved for use, as more research is needed to overcome limitations of these vaccines (Jiménez de Oya et al. 2019; Saiz 2020). Researchers have also noted the difficulty in administering a WNV vaccine to wild bird populations, as experimental oral vaccines that have been trialed have not yet been effective in protecting birds against the virus (Turell et al. 2003; Bunning et al. 2007).

To date, there is no vaccine to prevent avian salmonellosis in wild birds (Grunberg 2020). While clinical signs in infected birds can be treated with antibiotics, these may alter the birds' natural gut flora, making them vulnerable to re-infection (CWHL 2018a). Antibiotic treatments may also result in antimicrobial resistant *Salmonella* bacteria, and an increased risk of asymptomatic birds continuing to spread the disease among populations (CWHL 2018a; CWHC 2020). However, the likelihood of disease transmission can be reduced by regularly cleaning and disinfecting bird feeders, perches, and bird baths, or removing bird baths and feeders altogether, particularly in colder weather conditions, when *Salmonella* outbreaks in songbirds most frequently occur (CWHC 2020; CDFW 2021). Agencies also recommend reporting sick or dead birds to relevant government departments to help researchers monitor the size and spread of outbreaks (CWHC 2020; CDC 2021; CDFW 2021).

Several types of contraceptives have been developed for use in wild animal populations, which can assist in disease management by reducing the high risk of disease transmission associated with large populations (Massei & Cowan 2014). Surgical contraception has been used in some species, but this is an invasive method that is likely to cause distress, and carries the risks of pain, health complications, and death (Gray & Cameron 2010). Immunocontraception uses the antibodies in an animal's immune system to interfere with reproductive processes, such as sperm-egg binding, and prevent fertilization (Gray & Cameron 2010; Garside et al. 2014). Injectable immunocontraceptive vaccines have been effectively used to reduce populations of wild horses (Killian et al. 2006), wild elk (Shideler et al. 2002), and urban white-tailed deer (Rutberg & Naugle 2008). However, oral vaccines are thought to be the most practical administration method in large wild animal populations, as they are non-invasive, cost-effective, and, unlike injectable vaccines, do not carry the risk of adverse reactions at injection sites (Garside et al. 2014). Although oral vaccines have been developed, research is still being conducted to assess their effectiveness in wild animal populations (Massei 2018; Senar et al. 2021), and investigation into the associated impacts on behavior, health, and welfare is also required (Gray & Cameron 2010; Liedholm 2020).

In addition to reducing disease transmission rates, contraception can improve the wellbeing of wild animal populations by reducing the number of individuals suffering from poor welfare. Urban house sparrow chicks suffer from low survival rates, nutritional stress, and low body masses, while adult sparrows often exhibit signs of stress and poor body conditions in urban areas. By reducing numbers of urban house sparrows, suffering is also reduced as fewer individual sparrows will be born in environments where they are typically found to experience poor welfare. Using contraception to reduce numbers in large populations can also reduce competition, and improve the health of wild animals, as individuals are able to access more abundant and higher quality resources (Liedholm 2020).

Excluding animals from certain urban areas is another way to reduce wild animal suffering. While these strategies are often implemented to benefit human interests, they can also improve the welfare of wild animals by keeping them away from areas where they are vulnerable to injuries and mortalities or areas where they might harm other animals. Secure garbage cans, vent covers, chimney caps, and fillers and sealants for entry holes to buildings can reduce the risk of animals falling and becoming injured or trapped (Adams et al. 2005; Hadidian et al. 2007). Devices such as alarms, recordings of other animal noises, scarecrows, animal effigies, sprinklers, and lighting can be used to deter animals away from dangerous areas (Hadidian et al. 2007). Wild animals can also be discouraged from inhabiting high-risk urban areas by manipulating the composition of vegetation. Urban fox squirrels in Texas have shown a preference for areas with oak trees, so population numbers may be lowered by reducing the number of oaks in the area, and planting trees that squirrels seem to avoid, such as pines, bald cypress, and fruit trees (McCleery et al. 2007).

Adams et al. (2005) identified a lack of public awareness and education regarding urban animals and the agencies responsible for them as one of the main issues facing urban wild animal management. Educating and informing the public can benefit urban animal welfare directly, because when they are well informed, people are likely to become more willing to assist animals that need help, and less likely to contribute to further suffering. For example, negative attitudes and deliberate harms towards urban flying foxes are often associated with inaccurate public perceptions about health risks, and are likely to be reduced if more people become aware that the Hendra virus cannot be directly transmitted from flying foxes to humans (Kung et al. 2015). Education and public awareness can also have long-term impacts, such as increased interest and support for organizations, programs, and policies that contribute to improving urban animal welfare. A recent survey of scholars and students in life sciences found that there was strong support for research aimed at improving the welfare of wild animals in urban environments (Animal Ethics 2020b). This survey also revealed a lack of scientific knowledge concerning animal welfare among the respondents, demonstrating there is also a need to train and educate scientists and students in animal welfare science.

Future studies

A review by Brearley et al. (2013) found that many studies of urban wild animal diseases are based on one-dimensional comparisons between one site and another, and results showing the relationship between wild animal diseases and urban environments are rarely consistent. The authors suggest that incorporating spatial and temporal quantitative approaches would provide better insight into the variability and mechanisms of urban wild animal diseases. Studies of urban diseases and parasites are usually focused on their prevalence within populations, so research focused on the actual harms and sublethal effects suffered by infected animals is needed. Injuries resulting from competitive and aggressive interactions with conspecifics and other species are also understudied, particularly regarding their severity and how they impact the wellbeing of urban animals. An area for future studies to investigate is how different levels of urbanization impact the physiological conditions of urban animals, as well as their overall welfare, as no clear universal trends have been identified yet (Sepp et al. 2017).

Magle et al. (2019) observed that urban wild animal research is often limited by short-term studies that investigate one species in a single location. While this kind of information can be useful, it may only be applicable within a narrow context, as different cities vary in features such as size, geography, history, and topography (Pacione 2009), and individual animals are likely to respond to these variations in different ways (Aronson et al. 2016). The majority of urban animal research has also focused on birds and mammals, with little attention given to invertebrates, reptiles, and fishes (Marzluff et al. 2001; Magle et al. 2012). Fishes and other aquatic animals are particularly understudied, given that many urban areas are near to or include bodies of water such as oceans, lakes, and rivers (Birnie-Gauvin et al. 2016). These kinds of research limitations provide little insight into long-term urbanization effects, global patterns, or complex interactions between different urban animals, such as avoidance and competition (Magle et al. 2012; Magle et al. 2019). To better understand these processes, Magle et al. (2019) designed the Urban Wildlife Information Network (UWIN), that allows researchers in different cities to collect data and build long-term datasets on multiple species in urban environments. This information can be used to form theories and models related to urban welfare ecology, as most urban animal research has made ecological predictions based on models developed from non-urban areas, which often do not apply to urban environments (Magle et al. 2014). Data from UWIN can also be used to plan and design urban areas to meet the requirements of different urban wild animals, and assist in developing ways to improve their overall welfare.

Wild animal research has often involved capturing animals, and performing examinations and tests to assess their health and body conditions, or tagging and marking them for behavioral and demographic studies. The fear and stress associated with these methods are likely to have a negative impact on the behavior and wellbeing of the animals, as well as reducing the accuracy and reliability of research data (Jewell 2013). A range of non-invasive research techniques has been developed to gather information on wild animals without causing stress or altering their behavior. The distribution and abundance of populations can be assessed through observational counts of animals in plots and transects of urban areas (Adams et al. 2005). Citizen science projects also use observational methods to collect information on animals in residential areas, backyards, and feeders (Horn et al. 2002; Cornell Lab of Ornithology 2021). Drones, camera traps, and video recordings can be used to study population dynamics and how animals interact with each other and the urban environment (Royle & Gardner 2011; Di Cerbo & Biancardi 2013; Zemanova 2020). Smart nest-boxes with sensor devices can be used to weigh animals, and monitor their behavior (Larios et al. 2013). Alternatives to invasive blood and tissue sampling include DNA-based sampling from feces (Wilbert et al. 2015), hair (Sawaya et al. 2011), feathers (Olah et al. 2016), eggshells (Maia et al. 2017), spider webs (Blake et al. 2016), shed skin (Horreo et al. 2015), and skin-swabs (Prunier et al. 2012), which require little to no contact with the animals being studied (Zemanova 2020).

An important aspect in developing the field of urban welfare ecology is to determine how animal welfare will be assessed. Several methods have already been developed that could apply to urban wild animals. Biological indicators of health, such as disease and injury rates, can be used as a basis for assessing welfare (Savoie & Sarek 2018). These are less subjective than other measures, but can be difficult to determine in wild animals, as they will often hide signs of weakness, illness, or injury, to avoid appearing vulnerable to potential predators (Jordan 2005). Qualitative behavioral assessments (QBA) involve direct observation of an animal's behavior and body language, and how they interact with their environment (Wemelsfelder et al. 2001). This method is simple and easy to apply; however it has mostly been used to assess large mammals, and may be difficult to apply to less studied animals (Browning 2020). Different species may respond differently to fear, stress, and pain (Jordan 2005), so knowledge of their typical life-history and behavior in urban environments is needed for accurate welfare assessments. Academic models, such as the Five Domains Model (Mellor 2017), grade aspects such as nutrition, health, and behavior, which are then combined to see how they affect the overall wellbeing of the animal (Savoie & Sarek 2018; Browning 2020). These are comprehensive models that can be applied to a wide range of animals and conditions, but are based on grading systems that are subjective, making quantitative comparisons between assessments difficult (Savoie & Sarek 2018; Browning 2020). Future research should consider the ease of use, objectiveness, accuracy, and applicability across different types of situations, harms, and animals, when determining the best method or combination of methods for assessing urban animal welfare (Savoie & Sarek 2018).

In this study, we have examined what the lives of certain urban wild animals are like, but in the future, the field of urban welfare ecology could consider the overall wellbeing of all animals in urban environments. In addition to assessing the welfare of individual animals, this would also take into account the positive and negative effects that a particular animal has on the wellbeing of other animals. These assessments would examine interactions between different animals such as competition, predation, and symbiosis, and whether the presence of one animal results in other animals avoiding or being excluded from the same area. This information can then be used to evaluate how the presence of a particular animal contributes to more or less suffering in an urban environment, and inform decisions regarding how to reduce the overall suffering of all urban animals. For example, in this study we have found that house sparrows suffer from poor conditions in urban environments, including small body sizes, high levels of oxidative stress, predation from other animals, and poor nutrition in developing chicks. In comparison, urban pigeons experience little predation, and while some suffer from poor nutrition and foot deformities, we may conclude that they generally live better lives than house sparrows in urban environments. If the impact of house sparrows and urban pigeons on other animals is relatively equal, then urban policies to decrease house sparrow populations and encourage urban pigeons would contribute to less suffering overall. Through this kind of research in the developing field of urban welfare ecology, we can gain a better understanding about the lives of urban wild animals, and develop effective ways to improve their overall welfare.

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