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Overview article

So overt it's covert: Wildlife coloration in the city

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Abstract

With novel human–wildlife interaction, predation regimes, and environmental conditions, in addition to often fragmented and smaller populations, urban areas present wildlife with altered natural selection parameters and genetic drift potential compared with nonurban regions. Plumage and pelage coloration in birds and mammals has evolved as a balance between avoiding detection by predator or prey, sexual selection, and thermoregulation. However, with altered mutation rates, reduced predation risk, increased temperatures, strong genetic drift, and increased interaction with people, the evolutionary contexts in which these colorations arose are radically different from what is present in urban areas. Regionally alternative color morphs or leucistic or melanistic individuals that aren't typical of most avian or mammalian populations may become more frequent as a result of adaptive or neutral evolution. Therefore, I conceptualize that, in urban areas, conspicuous color morphologies may persist, leading to an increase in the frequency of regionally atypical pelage coloration. In the present article, I discuss the potential for conspicuous color morphs to arise and persist in urban mammalian and avian populations, as well as the mechanisms for such persistence, as a result of altered environmental conditions and natural selection pressures.

Keywords: coloration, evolution, urban ecology

Human-induced rapid environmental change is known to be a driver of evolutionary change in organisms during the Anthropocene (Sih et al. 2011, Hendry 2016, Alberti et al. 2017). As one of the most extreme examples of human-modified environments, urban areas serve as potential hotspots for rapid evolution (Donihue and Lambert 2015, Schell 2018, Rivkin et al. 2019, Diamond and Martin 2021, Lambert et al. 2021). Highly urbanized regions are characterized by increased human presence and impervious surfaces, as well as a lack of green space, high exposure to pollutants, high levels of artificial light and ambient noise, and increased temperatures (Grimm et al. 2008, MacDonnell et al. 2009, Imhoff et al. 2010, Niemelä 2011, Szulkin et al. 2020). In addition, urban areas typically have elevated levels of vehicle traffic, human–wildlife conflict, and physical landscape structures that may alter gene flow (e.g., habitat fragmentation, linear barriers) or mortality rates (e.g., vehicle collisions, conflict removals) within and among urban wildlife populations (Winchell et al. 2016, Johnson and Munshi-South 2017, Miles et al. 2019, Schell et al. 2021 Cosentino and Gibbs 2022). All these factors have been found to cause nonadaptive evolutionary phenotypic or genotypic responses in urban wildlife populations, and in select cases, scientists have even conclusively discovered adaptive evolution in response to the urban environment (Oke et al. 1973, Noël et al. 2006, Giraudeau et al. 2014, Serieys et al. 2015, Adducci et al. 2020, Campbell-Staton et al. 2020, Lambert et al. 2021, Cronin et al. 2022).

However, despite recent advancements in the field of urban evolutionary ecology, pelage coloration has been largely ignored (but see Leveau 2021). Coloration in birds and mammals serves many purposes, and several hypotheses have been proposed to explain the variation in plumage and pelage pattern and color (Caro 2005). Substantial evidence supports avoidance of detection, sexual selection and secondary fitness signaling, and thermoregulation as drivers of coloration (Roulin 2004, Caro 2005, Protas and Patel 2008, Stuart-Fox et al. 2017, Pembury Smith and Ruxton 2020). However, the interactions between these drivers are not well understood. With endothermic species, for example, how pelage and plumage coloration is affected by temperature is difficult to predict because of the numerous concurrent selection pressures and thermoregulatory mechanisms within the individuals. For example, desert-dwelling species might take on light colorations to reflect sunlight and blend into their surroundings, but many desert species are black in coloration (Buxton 1923, Caro 2008, Caro and Mallarino 2020). That being said, over large geographic scales, typical trends of coloration and pattern have evolved convergently in many different lineages around the globe, suggesting similar selection pressures throughout many different regions and time periods (Baker and Parker 1979, Caro 2005, Kronforst et al. 2012, Pembury Smith and Ruxton 2020). Despite pelage and plumage coloration's immense importance to a wide diversity of behavioral and physiological purposes, such as camouflage, territoriality, thermoregulation, and sexual selection signaling, a recent review of the impact of urbanization on coloration across taxa showed only 62 studies, 30 of which were spread across only three species (rock dove, also known as the domestic pigeon, *Columba livia*; great tit, *Parus major*; peppered moth, *Biston betularia*; Leveau 2021).

The present article builds on the literature on intraspecific pelage coloration (figure 1) evolution in both urban and nonurban systems to develop new hypotheses for how pelage and plumage coloration may change in urban areas. In this paragraph, I will lay out several hypotheses that will be addressed throughout the article (table 1; for a visual summary, see figure 2). I will explore the theoretical release from evolutionary constraints of novel pelage coloration phenotypes as an example of the potential for neutral or adaptive traits to persist in human-dominated

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Figure 1. Three images white-nosed coatis (***Nusua narica***). (a) An adult coati with normal pelage coloration and pattern blends into its surroundings. (b) A conspicuous adult coati with leucism does not blend into its surroundings. This adult leucitic coati was one of few individuals to display leucism in this population. (c) Multiple coatis foraging with normal coloration and two juvenile coatis exhibiting leucism. The photographs were taken on a golf course outside a resort, a place with few or no predators left for coatis, in Playa del Carmen, Quintana Roo, Mexico in 2018. Photographs: Samantha Kreling.

landscapes. I predict an increase in heritable rare pelage coloration as a result of increased exposure to toxins, pollutants, and chemical mutagens, in conjunction with strong genetic drift and higher densities of wildlife than in nonurban areas. In addition, I hypothesize that through the human shield effect and subsequent decreased predation pressure, changes in pelage coloration that would be negatively adaptive in nonurban areas may be neutral or beneficial in urban areas, allowing for alternative colorations to persist or even proliferate. Finally, there is potential for alternative color morphs to be selected for if they offer better thermoregulatory power to combat the increased heat load in urban areas, improve an individual's detoxification ability to mitigate increased toxin loads, or provide better visibility by humans to avoid direct human-mediated mortality (e.g., black squirrels are hit by cars less frequently than gray squirrels; Cosentino and Gibbs 2022).

Wildlife coloration in urban systems

In this section, I will review relevant literature and discuss the potential ways that urban wildlife may be released from the evolutionary constraints that drove the patterns of pelage and plumage coloration that we see in most wildlife (figure 3).

Genetic basis of mammalian and bird coloration

The mechanism for the deposition of pigment in bird feathers and mammalian fur is nearly identical (Lubnow 1963, van Grouw 2013). Coloration in both taxa is predominantly due to the pigments produced in cells known as *melanocytes* (Fox and Ververs 1960). These cells produce two types of melanin: Eumelanin is responsible for black, gray, and dark brown colors, and phaeomelanin is responsible for red and light brown colors (Lubnow 1963, Hoekstra 2006). Multiple genes regulate the production of these pigments (Lamoreux et al. 2010). Abnormalities in coloration that affect melanism can occur from single point mutations, often in the melanocortin 1 receptor (MC1R) or agouti (AGOUTI) genes (Lamoreux et al. 2010), and there are often multiple mutagenic pathways that may be responsible for the same or similar color aberrations (van Grouw and de Jong 2009, van Grouw 2017).

Genetic drift

Genetic drift may have signficant impacts on all of the hypotheses discussed in the present article on the feasibility of alternative coloration traits persisting in urban areas. The high levels of fragmentation, often small founding populations, and potential limitations to gene flow associated with urban areas means there is strong potential for genetic drift (Miles et al. 2019), or the

Table 1. Hypotheses and related mechanisms driving potential increases in conspicuous color morphs within urban environments.

Hypothesis title	Hypothesis	Mechanism
H1: Increased mutation load	Increased mutation load in urban areas leads to increase in individuals with aberrant color.	Air pollution and other toxic sources that are found at higher densities in urban areas induce germline heritable mutations.
H2: Founder effect	Populations founded by individuals with alternative coloration with little gene flow may create populations with high frequencies of these traits.	Limited gene flow into populations will amass traits found within the original founding individuals among the population.
H3: Low-nutrition diet	Low-nutrition diets may cause a nonheritable whitening of pelage.	Diets for wildlife in urban areas are typically composed of low-nutrition, high carbohydrate foods. This can lead to a lack of sufficient quantities of amino acids such as tyrosine, which are necessary to produce melanin, causing a lightening or whitening of pelage.
H4: Urban graying	High oxidative stress for wildlife in urban areas leads to nonheritable graying of pelage.	High stress environments such as that in urban areas causes increases in oxidative stress, leading to graying of pelage.
H5: Human shield	Predation constraints on pelage coloration will be lifted through lowered predation rates, resulting in an increase of conspicuous coloration.	Humans have for the most part eradicated large predators from urban areas. Although there are often higher densities of mesopredators in urban than nonurban areas, anthropogenic food supplementation results in lowered predation rates, releasing camouflage constraints in both predators and prey.
H6: Background-matching heterogeneity	Alternative color morphs that blend into anthropogenic backgrounds may be selected for in high predation environments.	In addition to the backgrounds for wildlife to match in wildland areas, urban areas have a variety of anthropogenically created backgrounds such as bricks and concrete. In cities with higher predation pressure, localized populations of wildlife with altered coloration that blend into selected backgrounds may be selected for.
H7: Human visibility	Conspicuous morphs may proliferate in areas of high human density and where visibility of the animal increases fitness or survival rate (i.e., nonconscious increased survival via humans).	Increased visibility of conspicuous individuals conveys advantage in the form of reduced mortality.
H8: Thermoregulation	Color morphs that offer thermoregulatory advantages will proliferate.	Urban areas are significantly warmer than rural areas. If the additional heat load is large enough to produce thermal stress on organisms, then color morphs that offer thermoregulatory benefits will be selected for.
H9: Melanistic detoxification	Melanistic morphs may have selective advantage through heavy metal detoxification.	Melanin binds certain heavy metal ions rendering them inert and storing them in structures such as fur or feathers, detoxifying the body. In urban areas in which toxin load is higher and may have significant fitness consequences, individuals that are better at detoxification may have a selective advantage.
H10: Sexual selection	Urbanization may alter sexual selection preferences related to coloration.	Sexual selection can be a strong selection force. If urbanization alters what individuals select for in a mate on the basis of coloration, then coloration in urban areas may regionally vary from nonurban conspecifics.
H11: Human interest	Conspicuous morphs may proliferate in areas of high human density and where humans give preferential treatment to conspicuous individuals (i.e., conscious increased survival via humans).	Preferential treatment to conspicuous individuals through physical protection and nutritional rewards may increase survival of conspicuous color morphs.
H12: Hybridization	Hybridization with domesticated animals may produce abnormal pelage coloration in wildlife.	Mating between wild animals and closely related domestic species may result in wildlife of abnormal coloration that may mimic coat colorations produced by leucism or melanism.
H13: Domestication syndrome	When wild animals are domesticated (intentionally or unintentionally), a variety of traits linked to behavioral states such as docility and boldness may be altered and produce variation within the “domestication suite,” including pelage coloration.	The “domestication suite” is a standard set of phenotypic traits that tend to be altered during the process of domestication. One of these traits is pelage coloration. Urban areas often select for bold wildlife individuals, and unintentional rewarding to these individuals may produce similar selection outcomes as intentional domestication.

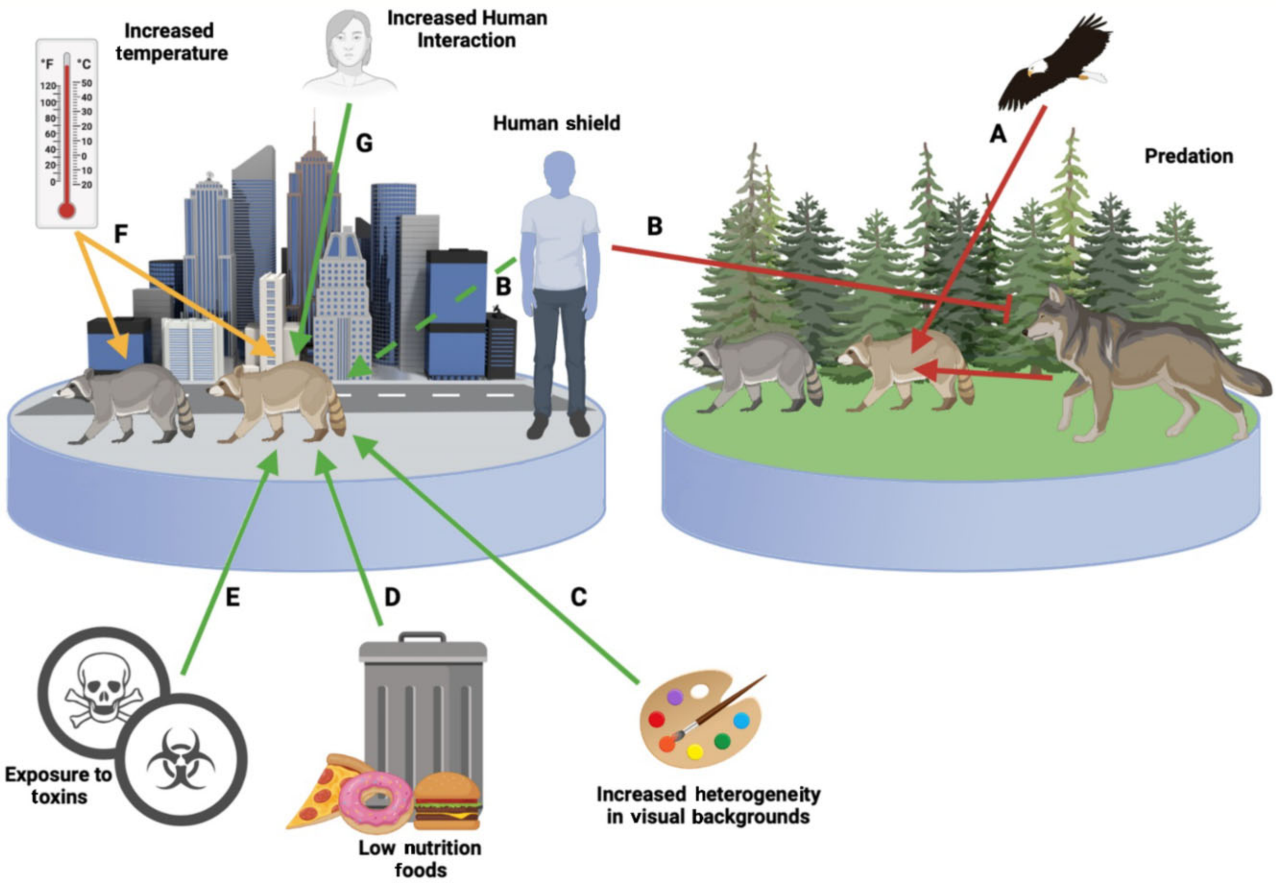

Figure 2. Conceptual figure to illustrate potential drivers and mechanisms influencing the theoretical release of novel coloration phenotypes in urban compared with rural areas. (a) Predators remove conspicuous individuals prior to breeding. (b) In urban areas, human presence directly or indirectly acts as a shield for prey and smaller carnivore species from large carnivores, reducing predation selection pressure. In addition, food supplementation for urban carnivores with anthropogenic resources may reduce predation risk. Combined removal of predation selection pressure releases novel phenotypes to persist in urban areas. (c) Where predation risk still exists, individuals with novel colorations have a higher probability of finding backgrounds that match their coloration because of a proliferation and wider variety of colors and textures across urban landscapes. (d). Low nutrition foods may provide a nonheritable cause for increase in novel coloration in birds and mammals. In particular, tyrosine deficiencies may present similar, but nonheritable, patterns to leucism. (e) Increased exposure to toxins and pollutants may increase mutation rates, giving rise to a potential increase in frequency of novel pelage phenotypes. (f) Increased temperatures may select for different pelage colorations that assist in thermoregulation. However, because of the complexity of thermoregulation in endotherms, the direction for this selection is difficult to predict. (g) Increased human visibility may result in direct reductions in mortality for conspicuous individuals or through increased interest in which conspicuous individuals are favored by human viewers as “novel” and “rare” sights.

random change in the frequency of alleles within a population (Fisher 1922, Wright 1945). The combination of increased mutation load and drift (e.g., founder effects, bottlenecks) or selection may lead to regionally elevated frequencies of different wildlife traits (Miles et al. 2019). Founder effects, a specific type of genetic drift, may have particularly strong effects on wildlife populations such that there may be limited population establishment events dependent on species attributes and corridor availability, which may be limited in urban areas (H1; Aziz and Rasidi 2014, Gallo et al. 2017, Kimmig et al. 2019). This could lead to elevated levels of certain phenotypes if the original founders possessed those traits or recessive alleles that may produce those characteristics in future generations (Boileau et al. 1992, Crispo et al. 2011). Indeed, we’ve seen strong population founder effects in the coat coloration of domestic cats based on settler origin in northeastern United States cities and cities across Europe (Todd 1964, 1966, Goncharenko and Zyat’kov 2012). For scenarios in which adaptive selection is occurring, its interactions with strong genetic drift in urban areas may either work to proliferate the mutations faster through the population by randomly dropping the frequency of typical coloration alleles. Alternatively, if there is only weak to moderate strength selection for alternative coloration, drift may outweigh selection timelines, and the population may randomly lose these new mutations. In addition, if the mutations causing abnormal coloration are recessive in nature, these alleles may be randomly lost in the population before the frequencies of the phenotypic trait are high enough for selection to engage (Andrews 2010, Lynch et al. 2016).

Mutation rate

Urban regions have concentrated historic and ongoing industrialization and development and are often littered with hotspots of chemical pollutant exposure (McDonnell et al. 1997, Apeagyei et al. 2011). In addition, urban areas have higher densities of humans and increased vehicular traffic, leading to elevated air pollution levels (Lawson et al. 2011, Cakmak et al. 2012, Da Silveira Fleck et al. 2014). Many of the most common types of

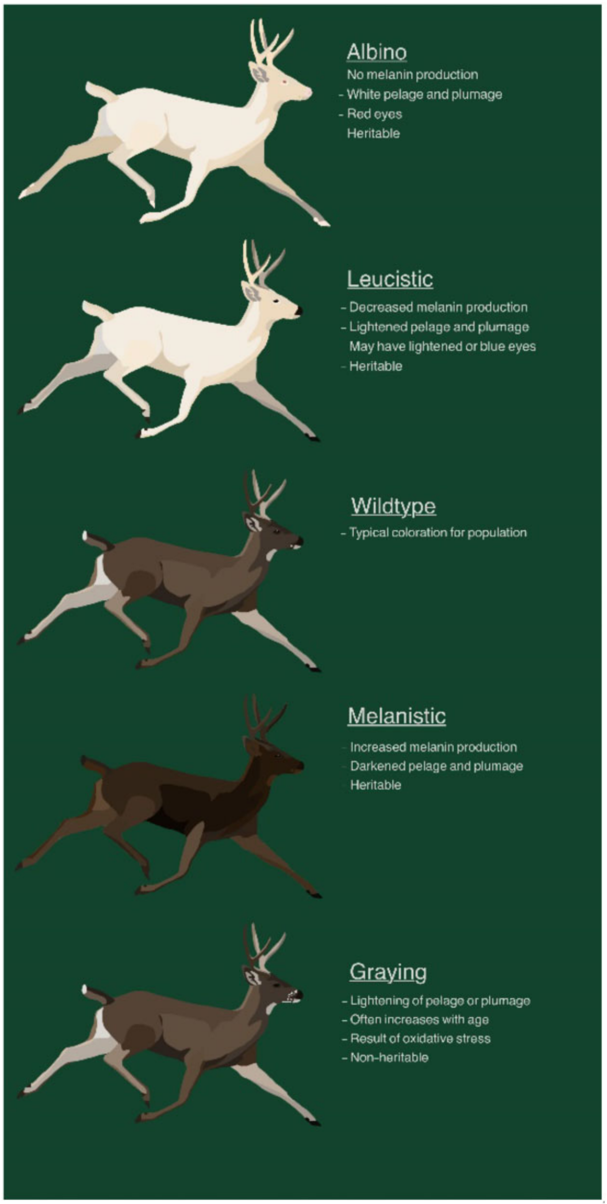

Figure 3. Examples of different coloration patterns that can occur because of increased (melanism) or decreased (leucism, albinism) melanin production and oxidative graying compared with wildtype or regionally “normal” coloration.

pollutants in urban areas are known carcinogens and mutagens (Cohen and Pope 1995, Turner et al. 2020) and have been demonstrated to increase the general mutation rate in both humans and animals (Ellegreen et al. 1997, Yauk et al. 2008, Dubrova 2019). Certain studies have also shown some of these mutations to be heritable (Yauk and Quinn 1996, Somers et al. 2002). With an increased mutation rate, novel phenotypes, including abnormal coloration of wildlife pelage, may arise more frequently in urban than in nonurban areas (H2). In addition, urban areas often host higher abundances of urban adapter species than rural regions (Tucker et al. 2020), increasing the likelihood that a mutation both occurs and is fixed by selection because of higher abundances of individuals (Kimura and Ohta 1971). Importantly, mutation itself is relatively weak as an evolutionary force. In order to proliferate within a population, mutations would either need to be under strong directional selection or occur at higher frequencies within a population because of genetic drift.

Importantly, there are also nongenetic or nonheritable causes of coloration abnormalities. Leucism, for example, may be caused by dietary deficiencies of tyrosine, an amino acid necessary for the synthesis of melanin (H3; van Grouw 2013). This is plausible because wildlife in urban areas have been found to have less nutritious diets than those in nonurban areas (Isaksson and Andersson 2007, Murray et al. 2015). Similarly, oxidative stress, which is found at higher levels in urban animals (Hutton and McGraw 2016), may lead to nongermline mutations in wildlife, causing graying or a lightening of coloration (H4; Møller and Mousseau 2001, Izquierdo et al. 2018). Finally, leucism may have negative effects for birds such that melanin deposits within their feathers provide mechanical strength to the structure and resistance to wear (Lee and Grant 1986, Bonser 1996, Kose and Møller 1999, Butler and Johnson 2004). Regardless, this presumed decrease in fitness may be negligible in the context of urban regions in which individuals typically have to travel smaller distances for food and face less predation risk (Berger 2007, Suraci et al. 2019, O’Donnell and delBarco-Trillo 2020, Sadoul et al. 2021).

Natural selection

For both predator and prey, camouflage can be imperative for survival (Pembury Smith and Ruxton 2020). Camouflage has been well documented as an antipredator mechanism for prey (Nachman et al. 2003, Caro 2005, Rosenblum et al. 2009, Stevens et al. 2011, Harris et al. 2020). Drivers of camouflage in predators have been less studied than antipredator responses for prey, but background matching crypsis can be important for successful hunting and overall fitness (Pembury Smith and Ruxton 2020).

Prey and some mesopredator species may be more abundant in urban areas as result of the human shield, the phenomenon in which the human presence and urbanization act as an inhibitor for apex predator establishment and persistence, allowing prey and smaller predatory species to thrive (Berger 2007, Geffroy et al. 2015, Suraci et al. 2019, Sadoul et al. 2021). Although an increase in mesopredators may seem problematic for conspicuous prey, research has shown that urban areas have decreased predation rates despite higher predator density because of anthropogenic food supplementation (Fischer et al. 2012, Eötvös et al. 2018). In nonurban settings with strong predation pressure, individuals that do not match their environments are easily spotted and removed from the population quickly (Belk and Smith 1996, Caro 2005). For example, species who experience camouflage mismatch due to climate change have seen significant declines because of increased predation, to the extent that some species such as the snowshoe hare may require evolutionary rescue to persist (Mills et al. 2013, Zimova et al. 2016). With less predation risk and therefore less need to blend in to avoid predation in urban regions, prey coloration may be released from these constraints (H5). Although mutations are rare, individuals with alternative coloration may be able to persist and even proliferate without predation removing individuals before they reproduce, especially if there is strong genetic drift (Miles et al. 2019).

Although predation pressures are generally reduced in urban areas, locations within cities may have regionally strong predation pressures. With higher levels of landscape heterogeneity than nonurban areas (Irwin and Bockstael 2007, Schell et al. 2020), urban areas have additional types of background patterns and colors that may allow for a greater variety of color morphs to exist while continuing to avoid predation through crypsis (figure 4, H6).

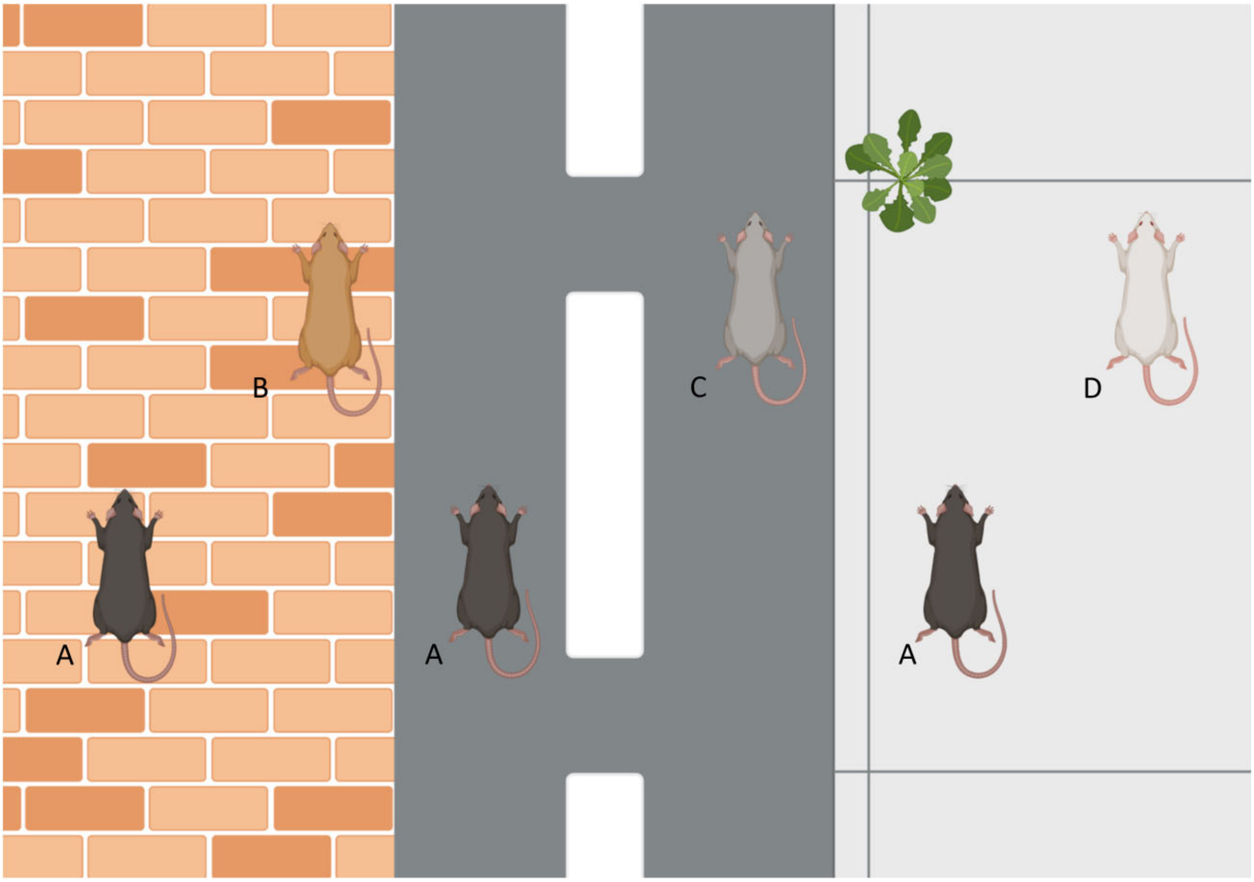

Figure 4. In addition to the background patterns and colorations found in natural habitat fragments in urban areas, urban areas offer a proliferation of human-created backgrounds that prey species may evolve to match to. This conceptual figure compares the typical coloration of black rats (rat A) to an alternative color morph (rats B, C, and D) that matches three common background colors and patterns in urban areas including bricks, asphalt, and concrete.

Urban areas typically have a greater variety of background types to match than nonurban areas. For example, urban areas typically have patches of naturalistic backgrounds that you would find in nonurban areas such as forest fragments and vegetated open spaces. In addition to these naturalistic backgrounds, several human-fabricated backgrounds such as brick, asphalt, concrete, and lawn are abundant in cities and can often cover vast areas contiguously (Leveau 2021). Selection via predation is most likely to occur in small-body prey species with high fecundity and that have relatively small home ranges, confining them to a particular environmental background color and pattern (Nachman et al. 2003, Rosenblum et al. 2009). For population-level change to occur, sufficiently high predation risk to select for individuals with aberrant color would be required. As an example of urban background pattern matching, Kettlewell (1955) documented selection for alternate color morphs in an urban area. Selection acted in favor of the more cryptic black peppered moths that blended into the trees that were covered with soot from nearby industrial factories, whereas light-color moths were easily identified and predated on.

Conspicuous coloration may even offer advantages over cryptic coloration in areas with little predation risk and where primary mortality is predominately from motor vehicle collisions or other visually mediated human-induced mortality sources (H7). This appears to be the case in Gibbs and colleagues (2019) where melanistic morphs of eastern gray squirrels (*Sciurus carolinensis*) dominate in the studied urban area and represented a disproportionately small percentage of roadkill. Recently, a multicity study showed repeated proliferation of melanistic morphs of this species over urban–rural clines. Notably, Cosentino and Gibbs (2022) also acknowledged that melanism was positively correlated with northward latitude, suggesting that the melanistic morph may have better thermotolerance for extreme cold temperatures in winter and that there may therefore be multiple selection pressures at play.

For predator species, access to anthropogenic foods may remove predation-based selection pressures for camouflage. In urban areas, wildlife species tend to supplement their diets with anthropogenic resources that are either intentionally or unintentionally left accessible (Contesse et al. 2004, Williams et al. 2006, Murray et al. 2015). This supplementation of food that does not require active pursuit may therefore loosen the predicted selection pressures on pelage coloration surrounding predator–prey relationships (Skelhorn and Rowe 2016, Pembury Smith and Ruxton 2020). As far as I am aware, no studies have addressed the frequencies of alternative color morphs in relation to predation regimes in urban areas.

For endotherms such as birds and mammals, the relationship between color and body temperature is complex and highly dependent on several factors, such as behavior, the structural properties of the feathers or hair, and the amount of fatty insulation (Walsberg 1983, Stuart-Fox et al. 2017). Coloration is further complicated by interacting selection pressures, such as predation avoidance and links to physiological processes (Cloudsley-Thompson 1999, Stuart-Fox et al. 2017). There are a few, albeit often contradictory, trends in endotherm coloration and thermal temperature (Stuart-Fox et al. 2017). For one, Gloger's rule specifies that endothermic animals are often darker in humid areas than in less humid regions, although this has also been attributed to additional benefits conferred by melanization, such as hydroregulation and UV protection (Gloger 1833, Burtt and Ichida 2004, Kamilar and Bradley 2011). Desert and other hot-ecosystem endotherms tend to either mirror the color of the soil and sand, a buff or sandy color, or tend to be black in coloration (Buxton 1923, Caro 2008, Caro and Mallarino 2020). Both coloration patterns may have potential benefits to animals in extreme ambient temperatures. As the amount of insulation in an individual declines, the potential effect of coat coloration on thermoregulation increases (Finch et al. 1980, Dawson et al. 2014).

Urban centers have a steep increase in impervious surface and a reduction in tree cover when compared with nonurban areas (Arnfield 2003). This leads to an average increase of 1.1–2 degrees Celsius in ambient temperatures in urban areas during the day (Hibbard et al. 2017, Allen et al. 2018). This increase in heat has already led to selection for thermal tolerant members in populations of urban anoles (Campbell-Staton et al. 2020). Although mechanisms that confer thermal tolerance in this population of anoles are not physically visible to the human eye, such as a change in pelage coloration would be, it suggests that urban heat islands could lead to selection for particular color phenotypes if they confer a thermoregulatory advantage (H8). For instance, if all things are held constant between two individuals with differing fur coloration, if one coloration provides better thermoregulatory power, it may be selected for in that environment. Interestingly, different color morphs may convey opposite effects, having positive benefits in freezing temperatures and negative effects in extreme heat conditions or vice versa, further complicating the potential of directional selection (Caro 2008, Hetem et al. 2009). As far as I found, the aforementioned study on melanization in squirrels across the eastern United States is the only mammalian study to look at a potential correlation between color morphology and ambient temperature in urban areas (Cosentino and Gibbs 2022). A single herpetological study showed some correlations between color polymorphism and temperature in a semiurban environment (Evans et al. 2020), but this has seemingly not been tested in other vertebrates or explicitly along an urban–rural gradient.

Individuals in urban areas are likely to have increased exposure to toxins and heavy metals, which have significant effects on fitness (Trust et al. 1990, Dauwe et al. 2004, Greenberg and Briemberg 2004, Snoeijs et al. 2004, Rainbow 2007, Eeva et al. 2009, Plum et al. 2010). The polymers that constitute melanin have negatively charged carboxyl, hydroxyl, and amine functional groups. These free electrons have been shown to bind to positive metal ions, acting as a detoxicant (Larson and Tjälve 1978, Liu et al. 2004, Bridelli and Crippa 2008). Melanistic morphs may therefore be able to detoxify their bodies by storing inert metal ions in melanin-laden structures such as feathers or fur (Chatelain et al. 2014). This mechanism has been suggested as a reason for more melanistic morphs of rock pigeons (*Columba livia*) in urban areas than in nonurban areas (Obukhova 2007, Chatelain et al. 2014, 2016).

Through this detoxification, melanin may indirectly improve immune functioning of individuals, because heavy metals will often weaken the immune system (McGraw 2003, Hong and Simon 2007, Chatelain et al. 2014, Serieys et al. 2018, Murray et al. 2019). For example, one study exposed rock pigeons with a variety of melaninization to zinc and lead. These studies showed that, although birds with more melanin retained a higher concentration of these heavy metals in their feather structures, their bloodwork showed metal concentrations similar to that of the lighter-color birds. However, darker juvenile birds had a higher survival rate than their light-color counter parts (Chatelain et al. 2016). This suggests that melanization does play some role in fitness and survivorship, potentially through detoxification, but the mechanism may be complex and mediated by other traits. Other studies have also shown a correlation between melanin and metal concentration in feather structures in white-tailed eagles and barn owls (Niecke et al. 1999, 2003). In addition, researchers have speculated that melanocytes play a direct role in vertebrate immunity and parasite resistance, although the mechanism is unclear (H9; Mackintosh 2011, Gasque and Jaffar-Bandjee 2015, Coté et al. 2018). Little experimental work has been done to understand the role of melanin in the immune system in wildlife, and most information that exists is entirely correlative.

Sexual selection

Urbanization may alter wildlife sexual selection preferences regarding coloration (H10). For the purposes of this article, sexual selection's implications for coloration primarily apply to avian species, because most mammalian species are not sexually dimorphic in color (Price 2006, McPherson and Chenoweth 2012, Cooney et al. 2019). Although many of the colors that are under sexual selection in birds are carotenoid based and derived from diet rather than melanin based (McGraw 2006), there are a few examples of altered sexual selection of melanin-based coloration in urban areas. Great tits (*Parus major*) in Barcelona, Spain, were found to have smaller black ties than forest birds. The tie is known to be a signal for sexual selection, and this was speculated to be a result of altered sexual selection in urban areas. However, Senar and colleagues (2014) also noted that birds with smaller ties were less exploratory and less bold and may have been selected in urban areas for these behavioral traits instead. White tail feathers in dark-eyed juncos (*Junco hyemalis*) are also a signal for sexual selection. An urban population in San Diego, California, had an average 22% decline in white plumage, which could be a result of altered sexual selection parameters (Yeh 2004). Notably, the authors mentioned that this result could also be due to genetic drift or phenotypic plasticity. Both examples show a decrease in coloration and sexual signaling. A recent review looking at which species of birds are likely to establish population in urban regions showed that species with less plumage dichromatism, when males are brighter in color than females, were more likely to inhabit urban areas (Iglesias-Carrasco et al. 2019). Although the review did not provide many conclusive reasons as to why species with less plumage dichromatism persist in cities more frequently, they theorized that production of color may be more costly in urban regions. Perhaps displaying fewer or smaller colorations in sexual signals mirrors this trend. Although there isn't much concrete evidence for altered sexual selection in avian species based on melanin-based coloration in urban areas, other sexually selected traits such as acoustic signals have been found to differ along an urban–rural gradient (Cronin et al. 2022). In European treefrogs (*Hyla arborea*; Troïanwski et al. 2015), painted gobies (*Pomatoschistus pictus*; de Jong et al. 2018), and common cuttlefish (*Sepia officinalis*; Kunc et al. 2014), altered coloration in noisy areas (e.g., urban) is thought to mitigate the effects of noise pollution on acoustic cues and mate selection; because birds also use calls to attract mates, this suggests that avian species could potentially alter coloration to attract mates in the presence of heavy noise pollution, where their calls are less likely to be heard by potential mates.

Human interest

Prior to the development of modern-day genetic techniques, scientists often categorized unique-color wildlife individuals as separate species. These "species" were often regarded as highly prized and rare (van Grouw 2017). Many cultures around the globe have similarly assigned significant value and importance to individuals and populations of wildlife with unique and conspicuous coloration (Saunders 1998, KnewWays 2010, Service et al. 2020). For example, the Kitasoo people of British Columbia have traditions and stories reaching back immemorial regarding *moksgm'ol*, leucistic black bears ("spirit bears") of the Great Bear Rainforest (Service et al. 2020). In addition, many areas in the US have bans on hunting leucistic or albino white-tailed deer (Wisconsin Department of Natural Resources 1940, Iowa General Assembly 1988, Illinois General Assembly 2021) and other leucistic wildlife (Stencel and Ghent 1987). Although melanistic wildlife individuals exist across the country, I could only identify protective laws for leucistic animals. The coloration of animals may also sway our willingness to conserve them from a psychological standpoint, prioritizing the things humans find aesthetically pleasing (Prokop and Randler 2018). Studies using community sourced pictures of aberrant-color birds showed that people were more likely to send in photos of birds with rare coloration than they were of less conspicuous color morphs because of their more unique coloration (Husby 2017, Zbyryt et al. 2020). Therefore, this increased visibility and inherent aesthetical fascination with conspicuous color morphs may lead to selective protection or beneficial behavior of humans toward individuals of conspicuous color (H11).

Behavior, hybridization, and domestication syndromes

Domestic animals exist at high densities alongside people in urban areas. Although it is unusual, hybridization between domestic animals and closely related wildlife species can occur (Adams et al. 2003, Chapman and Jones 2011, Leonard et al. 2014, Galov et al. 2015, Stronen et al. 2022). Hybridization in general, whether it be between two domestic species or a domestic and nondomestic species, can result in a variety of different pelage and plumage colorations (Hauffe et al. 2004, Schmutz et al. 2007, Zhang et al. 2014, Aguillon et al. 2021). With urban wildlife in close proximity to abundant domestic animals, there is the potential for hybridization to occur and introduce new coat or plumage phenotypes into the population (Adams et al. 2003). The high frequency of black-coated wolves in North America is a result of hybridization with domestic dogs and subsequent maintenance via heterozygote advantage and disease resistance (Wayne and vonHoldt 2012, Cubaynes et al. 2022). In European wolves, dark coloration is very rare, but it is typically associated with urbanization and the presence of feral dogs (Randi and Lucchini 2002). Recently, in Queens, New York, three coyotes were found to be recent (F1 and F2) hybrids with domestic dogs. Some of the offspring had extremely abnormal coat coloration as a result (Caragiulo et al. 2022). If these urban populations are small enough and with few enough migrants from other wild populations, these alternative colorations may be able to persist at a higher frequency than in nonurban populations (H12).

In addition, urban wildlife populations are preferentially established by individuals with bolder personalities (Caspi et al. 2022). In some species, melanin production is pleiotropically linked to behavior and is often associated with bolder and more exploratory behavior (Ducrest et al. 2008, Mateos-Gonzalez and Senar 2012). Bolder individuals that are more likely to approach humans and adapt to the novelty of urban environments may be selected for once they are established as well (Brooks et al. 2020). Selection for these individuals that tolerate humans and may even lose their fear of humans, mimics domestication studies such as the infamous Russian silver fox farm experiments. These experiments showed that selection for less fearful and bolder animals eventually lead to domestication and, as by-products of domestication—a variety of phenotypic traits, the domestication syndrome—that were not frequent or present in the wild individuals became common (Trut 1999, Hare et al. 2005, Hare and Tomasello 2005, Wilkins et al. 2014). One of these byproducts was changes in coat coloration, such as piebald coloration, white feet, chest spots, and tail tips (Trut 1999, Wilkins et al. 2014). Over time, unintentional selection for individuals that are bolder in urban areas may develop alternative coat coloration as a byproduct of unintentional domestication similar to the self-domestication hypothesis for wolves (H13; Hare and Tomasello 2005, Hare 2017). Brooks and colleagues (2020) addressed this question in coyotes (*Canis latrans*) and similar to earlier work showed that urban coyotes are bolder than their rural conspecifics (Breck et al. 2019) but failed to confirm higher frequencies of domestication syndrome coat phenotypes in urban coyotes.

Discussion, implications, and future work

In this section, I review the potential implications of wildlife having aberrant color in cities and address how scientists can begin to assess trends in coloration across urban–rural gradients.

Why aren't we seeing high rates of aberrant-color wildlife in all urban areas?

Ultimately, the selection pressures that influence pelage coloration in wildlife are complex and interacting. Many of the stated hypotheses are dependent on strong genetic drift and limited gene flow from wildland populations to allow for the proliferation of wildlife with abnormal coloration. In addition, mutations in general are relatively infrequent, and typically have adverse effects. The chances of MC1R or AGOUTI mutations causing abnormal coloration are, therefore, rare in general. We may not be seeing aberrant-color wildlife in all urban regions because these mutations may simply have rarely occurred in urban areas and not had the chance to persist or were not coupled with strong enough genetic drift or selection in their respective environments to allow for proliferation. Similarly, there are varying selection pressures among and within different cities. If predation pressure is still high in some cities or parts of cities, conspicuous individuals are unlikely to persist there, because they would likely be removed from the population before reproduction. In addition, alternative color morphs may have unknown underlying physiological differences that affect fitness negatively. Even if these individuals with regionally abnormal color exist and are in the correct genetic landscape to allow persistence, if there are unknown negative consequences that affect fitness or survival, they will likely not thrive in the population. On the other hand, if abnormal coloration conveys fitness or survival advantages on one axis of selection, with a multitude of selection pressures influencing wildlife coloration, advantages conveyed by alternative pelage coloration must strongly outweigh any potential opposing selection pressures. Finally, on evolutionary time scales, cities are a relatively new landscape, and studying wildlife in urban areas is an even more recent development. Scientists likely have little idea of what the frequency of different color morphs in urban and nonurban areas is. This subject has rarely been studied, and the hypotheses suggested in the present article are all in need of further research.

Implications

Physical appearances in wildlife serve distinct and important purposes. From sexual selection and secondary fitness signaling to antidetection mechanisms, pelage pattern and coloration help determine the survival and reproductive success of individuals. Given time and the correct genetic landscape, urban areas may allow or even select for alternative color morphs. However, proliferation of conspicuous color morphs due to one mechanism may have dramatic implications for the other purposes of pelage coloration.

The unintended consequences of human-mediated selection may have vast and wide-ranging effects on wildlife populations. For example, laws that protect leucistic and albino wildlife may encourage proliferation of these specific color morphs. There are multiple states in the United States with protections on wildlife with abnormal coloration (Wisconsin DNR 1940, Iowa General Assembly 1988). Even at the municipal level, there are towns that provide protections to these individuals with alternative color, such as for white morphs of Eastern gray squirrels in Olney, Illinois (City of Olney municipal code 6.12.020.B). Towns like Olney (e.g., Marionville, Mississippi, United States; Marysville, Kansas, United States; Kenton, Tennessee, United States; Kent, Ohio, United States; Exeter, Ontario, Canada) even profit from these individuals of unique color through tourism, incentivizing their protection. However, protection of these individuals may have unintended population consequences. Leucism and albinism have been linked to potentially negative health and fitness outcomes in wildlife, such as weakened feathers in birds or may be the result of inbreeding as seen in domestically raised white tigers (Lee and Grant 1986, Bonser 1996, Kose and Møller 1999, Butler and Johnson 2004, Xu et al. 2013). Therefore, artificially selecting for these color morphs could significantly decrease the average fitness of these populations, making them more vulnerable to human and climate-related disturbances.

In addition, with the many behavioral and physiological roles that wildlife pelage and plumage coloration plays, selection for individuals with aberrant colors on one axis may have negative consequences on another. For example, if individuals with aberrant color are selected for in cities on the basis of a thermoregulatory advantage, how will this affect secondary fitness signaling and mate selection? In addition, if individuals with aberrant color are selected for on the basis of withstanding the greater temperatures found in urban heat islands, they may be more susceptible to climate volatility and sudden cold snaps that may present themselves more frequently as climate change progresses and daily weather patterns becomes less predictable (Sheshardri et al. 2021).

Finally, there has been a global increase in human–wildlife conflict in recent decades, which is predicted to only get worse with climate change (Abrahms 2021, Schell et al. 2021). In urban areas, people are often at closer proximity to wildlife than nonurban areas. If people begin favoring wildlife individuals with alternative coloration, through protective laws or supplemental feeding, the proximity to these individuals may further increase, leading to higher likelihoods of conflict arising (Thirgood et al. 2005). In addition, if alternative coloration is caused nongenetically, such as through urban graying or low nutrition foods, these individuals may be more susceptible to accumulating pathogens or diseases as a result of lowered immune responses (Murray et al. 2019). Coupled with close proximity to humans, this could potentially increase the risk of disease spillover (Murray et al. 2019, Messmer 2020).

Future studies

Although Leveau (2021) found more than 60 studies that, to some extent, addressed frequencies of different color morphs between urban and nonurban regions, the vast majority of these studies were concentrated on just three species. Addressing pelage and plumage coloration frequency across different study systems and taxa will be imperative for understanding the likelihoods of proliferation for different phenotypes. In addition, few of the hypotheses I suggest above have been studied at all. I suggest that researchers prioritize understanding how environmental change due to urbanization can alter the strength and direction of adaptive and nonadaptive evolutionary forces across phenotypic traits. Urban evolutionary ecology is a nascent field and urban adaptive and nonadaptive evolution is therefore poorly understood. I suggest building on literature regarding urban evolution in general and applying these findings to coloration morphology specifically. Although the focus is beginning to change, to date, much of the research on urban wildlife evolution has been conceptual in nature or correlative rather than mechanistic (Diamond and Martin 2021, Lambert et al. 2021). Much more research on the mechanisms behind adaptation or regional genetic changes in urban wildlife is needed. In addition, those studies that did look at urban evolution have primarily been focused on specific locales and have lacked replication across urban areas (Lambert et al. 2021).

Scientists should leverage existing museum collections, camera trap networks (Urban Wildlife Information Network), community science data (Zbyryt et al. 2020, Cosentino and Gibbs 2022), and census data (e.g., the Squirrel Census) to begin to monitor and understand the phenotypic frequencies of different color morphs across urban–rural gradients. In addition, conducting laboratory studies may help us understand when atypical color morphs may be advantageous. Borrowing methods from studies such as Campbell-Staton and colleagues (2020), scientists can conduct thermal tolerance studies to understand how pelage and plumage color morphology affects heat load in different thermal environments. Similarly, laboratory experiments can help us further understand how exposure to different chemicals and mutagens may influence mutation load and subsequent heritability of those mutations and whether there are any biases in the genetic regions they are likely to mutate within. Exposing laboratory animals to polluting compounds common in urban areas (e.g., lead, various hydrocarbons, fine particulate matter) and tracking potential genetic changes will help us understand the likelihood of different mutations, such as those that produce coloration changes. Finally, although they are difficult to enact, transplant experiments with individuals of atypical color between urban and nonurban conditions could help us understand how predation pressures and general environmental conditions influence survival and the reproduction rates of these individuals.

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References

Abrahms B. 2021. Human–wildlife conflict under climate change. *Science* 373: 484–485.

Adams JR, Leonard JA, Waits LP. 2003. Widespread occurrence of a domestic dog mitochondrial DNA haplotype in southeastern US coyotes. *Molecular Ecology* 12: 541–546.

Adducci A II, Jasperse J, Riley S, Brown J, Honeycutt R, Monzón J. 2020. Urban coyotes are genetically distinct from coyotes in natural habitats. *Journal of Urban Ecology* 6: juaa010.

Aguillon SM, Walsh J, Lovette IJ. 2021. Extensive hybridization reveals multiple coloration genes underlying a complex plumage phenotype. *Proceedings of the Royal Society B* 288 20201805.

Alberti M, Correa C, Marzluff JM, Hendry AP, Palkovacs EP, Gotanda KM, Hunt VM, Apgra TM, Zhou Y. 2017. Global urban signatures of phenotypic change in animal and plant populations. *Proceedings of the National Academy of Sciences* 114: 8951–8956.

Allen MR, et al. 2018. Framing and Context. Pages 49–92 in Masson-Delmotte V et al., eds. *Global Warming of 1.5°C: An IPCC Special Report on the Impacts of Global Warming of 1.5°C above Pre-industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty*. Cambridge University Press.

Andrews CA. 2010. Natural selection, genetic drift, and gene flow do not act in isolation in natural populations. *Nature Education Knowledge* 3: 5.

Arnfield AJ. 2003. Two decades of urban climate research: A review of turbulence, exchanges of energy and water, and the urban heat island. *International Journal of Climatology* 23: 1–26.

Apeagyei E, Bank MS, Spengler JD. 2011. Distribution of heavy metals in road dust along an urban–rural gradient in Massachusetts. *Atmospheric Environment* 45: 2310–2323.

Aziz HA, Rasidi MH. 2014. The role of green corridors for wildlife conservation in urban landscape: A literature review. *Earth and Environmental Science* 18: 012093.

Baker RR, Parker GA. 1979. The evolution of bird coloration. *Philosophical Transactions of the Royal Society B* 287: 63–130.

Belk MC, Smith MH. 1996. Pelage coloration in oldfield mice (*Peromyscus polionotus*): Antipredator adaptation? *Journal of Mammalogy* 77: 882–890.

Berger J. 2007. Fear, human shields, and the redistribution of prey and predators in protected areas. *Biology Letters* 3: 620–623.

Boileau MG, Herbert PDN, Schwartz SS. 1992. Non-equilibrium gene frequency divergence: Persistent founder effects in natural populations. *Journal of Evolutionary Biology* 5: 25–39.

Bonser RHC. 1996. The mechanical properties of feather keratin. *Journal of Zoology* 239: 477–484.

Breck SW, Poessel SA, Mahoney P, Young JK. 2019. The intrepid urban coyote: A comparison of bold and exploratory behavior in coyotes from urban and rural environments. *Scientific Reports* 9: 2104.

Bridelli M, Crippa P. 2008. Theoretical analysis of adsorption of metal ions to the surface of melanin particles. *Adsorption* 14: 101–109.

Brooks J, Kays R, Hare B. 2020. Coyotes living near cities are bolder: Implications for dog evolution and human–wildlife conflict. *Behaviour* 157: 289–313.

Burtt EH, Ichida JM. 2004. Gloger's rule, feather degrading bacteria, and color variation among song sparrows. *Condor* 106: 681–686.

Butler M, Johnson AS. 2004. Are melanized feather barbs stronger? *Journal of Experimental Biology* 207: 285–293.

Buxton PA 1923. *Animal Life in Deserts: A Study of the Fauna in Relation to the Environment*. Arnold.

Cakmak S, Mahmud M, Grgicak-Mannion A, Dales RE. 2012. The influence of neighborhood traffic density on the respiratory health of elementary schoolchildren. *Environment International* 39: 128–132.

Campbell-Staton SC, Winchell KM, Rochette NC, Fredette J, Maayan I, Schweizer RM, Catchen J. 2020. Parallel selection on thermal physiology facilitates repeated adaptation of city lizards to urban heat islands. *Nature Ecology and Evolution* 4: 652–658.

Caragiulo A, Gaughran SJ, Duncan N, Nagy C, Weckel M, vonHoldt BM. 2022. Coyotes in New York City carry variable genomic dog ancestry and influence their interactions with humans. *Genes* 13: 1661.

Caro T. 2005. The adaptive significance of coloration in mammals. *BioScience* 55: 125–136.

Caro T. 2009. Contrasting coloration in terrestrial mammals. *Philosophical Transactions of the Royal Society B* 364: 537–548.

Caro T, Mallarino R. 2020. Coloration in mammals. *Trends in Ecology and Evolution* 35: 357–366.

Caspi T, Johnson JR, Lambert MR, Schell CJ, Sih A. 2022. Behavioral plasticity can facilitate evolution in urban environments. *Trends in Ecology and Evolution* 37: 1092–1103.

Chapman R, Jones D. 2011. Foraging by native and domestic ducks in urban lakes: Behavioral implications of all that bread. *Corella* 35: 101–106.

Chatelain M, Gasparini J, Jacquin L, Frantz A. 2014. The adaptive function of melanin-based plumage coloration to trace metals. *Biology Letters* 10: 20140164.

Chatelain M, Gasparini J, Frantz A. 2016. Trace metals, melanin-based pigmentation and their interaction influence immune parameters in feral pigeons (*Columbia livia*). *Ecotoxicology* 25: 521–529.

Cloudsley-Thompson JL. 1999. Multiple factors in the evolution of animal coloration. *Naturwissenschaften* 86: 123–132.

Cohen AJ, Pope CA. 1995. Lung cancer an air pollution. *Environmental Health Perspectives* 103: 219–224.

Contesse P, Hegglin D, Gloor S, Bontadina F, Deplazes P. 2004. The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mammalian Biology* 69: 81–95.

Cooney CR, Varley ZK, Nouri LO, Moody CJA, Jardine MD, Thomas GH. 2019. Sexual selection predicts the rate and direction of colour divergence in a large avian radiation. *Nature Communications* 10: 1773.

Cosentino BJ, Gibbs JP. 2022. Parallel evolution of urban–rural clines in melanism in a widespread mammal. *Scientific Reports* 12: 1752.

Coté J, Boniface A, Blanchet S, Hendry AP, Gasparini J, Jacquin L. 2018. Melanin-based coloration and host–parasite interactions under global change. *Proceedings of the Royal Society B* 285: 20180285.

Crispo E, Moore J, Lee-Yaw JA, Gray SM, Haller BC. 2011. Broken barriers: Human-induced changes to gene flow and introgression in animals. *BioEssays* 33: 508–518.

Cronin AD, Smit JAH, Muñoz MI, Poirier A, Moran PA, Jerem P, Halfwerk W. 2022. A comprehensive overview of the effects of urbanisation on sexual selection and sexual traits. *Biological Reviews* 97: 1325–1345.

Cubaynes S et al. 2022. Disease outbreaks select for mate choice and coat color and wolves. *Wildlife Disease* 378: 300–303.

Da Silveira Felck A, Vieira M, Amantéa SL, Rhoden CR. 2014. A comparison of the human buccal cell assay and the pollen abortion assay in assessing genotoxicity in an urban–rural gradient. *International Journal of Environmental Research and Public Health* 11: 8825–8838.

Dauwe T, Janssens E, Kempenaers B, Eens M. 2004. The effect of heavy metal exposure on egg size, eggshell thickness and the number of spermatozoa in blue tit *Parus caeruleus* eggs. *Environmental Pollution* 129: 125–129.

Dawson TJ, Webster KN, Maloney SK. 2014. The fur of mammals in exposed environments: Do crypsis and thermal needs necessarily conflict? The polar bear and marsupial koala compared. *Journal of Comparative Physiology B* 184: 273–284.

de Jong K, Amorim MCP, Fonseca PJ, Heubel KU. 2018. Noise affects multimodal communication during courtship in a marine fish. *Frontiers in Ecology and Evolution* 6: 113.

Diamond SE, Martin RA. 2021. Evolution in cities. *Annual Review of Ecology, Evolution, and Systematics* 52: 519–540.

Donihue CM, Lambert MR. 2015. Adaptive evolution in urban ecosystems. *AMBIO* 44: 194–203.

Dubrova Y. 2019. Mutation induction in humans and mice: Where are we now? *Cancers* 11: 1708.

Ducrest AL, Keller L, Roulin A. 2008. Pleiotropy in the melanocortin system, colouration and behavioral syndromes. *Trends in Ecology and Evolution* 23: 502–510.

Eeva T, Aloha M, Lehikoinen E. 2009. Breeding performance of blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) in a heavy metal polluted area. *Environmental Pollution* 157: 3126–3131.

Ellegreen H, Lindgren G, Primmer CR, Møller AP. 1997. Fitness loss and germline mutations in barn swallows breeding in Chernobyl. *Nature* 389: 593–596.

Eötvös CB, Magura T, Lövei GL. 2018. A meta-analysis indicates reduced predation pressure with increasing urbanization. *Landscape and Urban Planning* 180: 54–59.

Evans AE, Urban MC, Jockusch EL. 2020. Developmental temperature influences color polymorphism but not hatchling size in a woodland salamander. *Oecologia* 192: 909–918.

Finch VA, Dmi'el R, Boxman R, Shkolnik A, Taylor CR. 1980. Why black goats in hot deserts? Effects of coat color on heat exchanges of wild and domestic goats. *Physiological Zoology* 53: 19–25.

Fischer JD, Cleeton SH, Lyons TP, Miller JR. 2012. Urbanization and the predation paradox: The role of trophic dynamics in structuring vertebrate communities. *BioScience* 62: 809–818.

Fisher RA. 1923. On the dominance ratio. *Proceedings of the Royal Society of Edinburgh* 42: 321–341.

Fox HM, Vevers G. 1960. *The Nature of Animal Colors*. Sidgwick and Jackson.

Gallo T, Fidino M, Lehrer EW, Magle SB. 2017. Mammal diversity and metacommunity dynamics in urban green spaces: Implications for urban wildlife conservation. *Ecological Applications* 27: 2330–2341.

Galov A, Fabbri E, Caniglia R, Arbanasić H, Lapalombella S, Florijančić T, Bošković I, Galaverni M, Randi E. 2015. First evidence of hybridization between golden jackal (*Canis aureus*) and domestic dog (*Canis familiaris*) as revealed by genetic markers. *Royal Society Open Science* 2: 150450.

Gasque P, Jaffar-Bandjee MC. 2015. The immunology and inflammatory response of human melanocytes in infectious diseases. *Journal of Infection* 71: 413–421.

Geffroy B, Samia DSM, Bessa E, Blumstein DT. 2015. How nature-based tourism might increase prey vulnerability to predators. *Trends in Ecology and Evolution* 30: 755–765.

Gibbs JP, Buff MF, Cosentino BJ. 2019. The biological system: Urban wildlife, adaptation, and evolution: Urbanization as driver of contemporary evolution in gray squirrels (*Sciurus carolinensis*). Pages 269–286 in Hall MHP Balogh SB, eds. *Understanding Urban Ecology: An Interdisciplinary Systems Approach*. Springer.

Giraudeau M, Nolan PM, Black CE, Earl SR, Hasegawa M, McGraw KJ. 2014. Song characteristics track bill morphology along a gradient of urbanization in house finches (*Haemorhous mexicanus*). *Frontiers in Zoology* 11: 83.

Gloger CL. 1833. Das Abändern der Vögel durch Einfluss der Klima's. A. Schulz.

Goncharenko GG, Zyat'kov SA. 2012. Level of genetic differentiation in cats (*Felis cattus* L.) in Western Europe, North America, and Eastern European populations. *Russian Journal of Genetics: Applied Research* 2: 47–52.

Greenberg S, Briemberg H. 2004. A neurological and hematological syndrome associated with zinc excess and copper deficiency. *Journal of Neurology* 251: 111–114.

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM 2008. Global change and the ecology of cities. *Science* 319: 756–760.

Hare B. 2017. Survival of the friendliest: *Homo sapiens* evolved via selection for prosociality. *Annual Review of Psychology* 68: 155–186.

Hare B, Tomasello M. 2005. Human-like social skills in dogs? *Trends in Cognitive Sciences* 9: 439–444.

Hare B, Plyusnina I, Ignacio N, Schepina O, Stepika A, Wrangham R, Trut L. 2005. Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology* 15: 226–230.

Harris RB, Irwin K, Jones MR, Laurent S, Barrett RDH, Nachman MW, Good JM, Linnen CR, Jensen JD, Pfeifer SP. 2020. The population genetics of crypsis in vertebrates: Recent insights from mice, hares, and lizards. *Heredity* 124: 1–14.

Hauffe HC, Panithanarak T, Dallas JF, Piálek J, Gündüz I, Searle JB. 2004. The tobacco mouse and its relatives: A "tail" of coat colors, chromosomes, hybridization, and speciation. *Cytogenetic and Genome Research* 105: 395–405.

Hendry AP. 2016. *Eco-evolutionary Dynamics*. Princeton University Press.

Hetem RS, de Witt BA, Fick LG, Fuller A, Kerley GIH, Meyer LCR, Mitchell D, Maloney SK. 2009. Body temperature, thermoregulatory behavior and pelt characteristics of three colour morphs of springbok (*Antidorcas marsupialis*). *Comparative Biochemistry and Physiology A* 152: 379–388.

Hibbard KA, Hoffman FM, Huntzinger D, West TO. 2017. Changes in land cover and terrestrial biogeochemistry. Pages 277–302 in Wuebbles DJ, Fahey DW, Hibbard KA, Dokken DJ, Stewart BC Maycock TK, eds.*Climate Science Special Report: Fourth National Climate Assessment*, vol. 1. US Global Change Research Program.

Hoekstra HE. 2006. Genetics, development and evolution of adaptive pigmentation in vertebrates. *Heredity* 97: 222–234.

Hong L, Simon JD. 2007. Current understanding of the binding sites, capacity, affinity, and biological significance of metals in melanin. *Journal of Physical Chemistry B* 111: 7938–7947.

Husby M. 2017. Colour aberrations in Eurasian magpies *Pica pica* in Europe. *Ornithological Science* 16: 111–119.

Hutton P, McGraw KJ. 2016. Urban impacts on oxidative balance and animal signals. *Fronteirs in Ecology and Evolution* 4.https://www.frontiersin.org/articles/10.3389/fevo.

Iglesias-Carrasco M, Duchêne DA, Head ML, Møller AP, Cain K. 2019. Sex in the city: Sexual selection and urban colonization of passerines. *Biology Letters* 15: 20190257.

Illinois General Assembly. 2021. SB1248 102^{nd} General Assembly. Wildlife Code section 2.24.Illinois General Assembly.

Imhoff ML, Zhang P, Wolfe RE, Bounoua L. 2010. Remote sensing of the urban heat island effect across biomes in the continental USA. *Remote Sensing of Environment* 114: 504–513.

Iowa General Assembly. 1988. 481A.124 Taking predominantly white deer of the whitetail species prohibited. Laws of the Seventy-Second General Assembly, chapter 1184.Iowa General Assembly.

Irwin EG, Bockstael NE. 2007. *The evolution of urban sprawl: Evidence of spatial heterogeneity and increasing landscape fragmentation*. Proceedings of the National Academy of Sciences 104: 20672–20677.

Isaksson C, Andersson S. 2007. Carotenoid diet and nestling provisioning in urban and rural great tits *Parus major*. *Journal of Avian Biology* 38: 564–572.

Izquierdo L, Thomson RL, Aguirre JI, Díez-Fernández A, Faivre B, Figuerola J, Ibáñez-Álamo JD. 2018. Factors associated with leucism in the common blackbird *Turdus merula*. *Journal of Avian Biology* 49: e01778.

Johnson MTJ, Munshi-South J. 2017. Evolution of life in urban environments. *Science* 358: eaam8327.

Kamilar JM, Bradley BJ. 2011. Interspecific variation in primate coat colour supports Gloger's rule. *Journal of Biogeography* 38: 2270–2277.

Kettlewell HBD. 1955. Selection experiments on industrial melanism in the *Lepidoptera*. *Heredity* 9: 323–342.

Kimmig SE, et al. 2019. Beyond the landscape: Resistance modelling infers physical and behavioral gene flow barriers to a mobile carnivore across metropolitan areas. *Molecular Ecology* 29: 466–484.

Kimura M, Ohta T. 1971. On the rate of molecular evolution. *Journal of Molecular Evolution* 1: 1–17.

KnewWays. 2010. Chief Arvol Looking Horse Speaks of White Buffalo Prophecy. YouTube (27 August 2010). www.youtube.com/watch?v=PHqVdZmpRgI.

Kose M, Møller AP. 1999. Sexual selection, feather breakage and parasites: The importance of white spots in the tail of the barn swallow (*Hirundo rustica*). *Behavioral Ecology and Sociobiology* 45: 430–436.

Kronforst MR, Barsh GS, Kopp A, Mallet J, Monteiro A, Mullen SP, Protas M, Rosenblum EB, Schneider CJ, Hoekstra HE. 2012. Unraveling the thread of nature's tapestry: The genetics of diversity and convergence in animal pigmentation. *Pigment Cell and Melanoma Research* 25: 411–433.

Kunc HP, Lyons GN, Sigwart JD, McLaughlin KE, Houghton JDR. 2014. Anthropogenic noise affects behavior across sensory modalities. *American Naturalist* 184: E93–E100.

Lambert MR, Brans KI, Des Roches S, Donihue CM, Diamond SE. 2021. Adaptive evolution in cities: Progress and misconceptions. *Trends in Ecology and Evolution* 36: 239–257.

Lamoreux ML, Delmas V, Larue L, Bennett D. 2010. *The Colors of Mice: A Model Genetic Network*. Wiley-Blackwell.

Larson B, Tjälve H. 1979. Studies on the mechanism of drug-binding to melanin. *Biochemical Pharmacology* 28: 1181–1187.

Lawson SJ, Galbally IE, Powell JC, Keywood MD, Molloy SB, Cheng M, Selleck PW. 2011. The effect of proximity to major roads on indoor air quality in typical Australian dwellings. *Atmospheric Environment* 45: 2252–2259.

Leonard JA, Echegaray J, Randi E, Vilá C. 2014. Impact of hybridization with domestic dogs on the conservation of wild canids. Pages 170–184 in Gompper ME, ed. *Free-Ranging Dogs and Wildlife Conservation*. Oxford University Press.

Leveau L. 2021. United colours of the city: A review about urbanisation impact on animal colours. *Austral Ecology* 46: 670–679.

Lee DS, Grant GS. 1986. An albino greater shearwater: Feather abrasion and flight energetics. *Wilson Bulletin* 98: 488–490.

Liu Y, Hong L, Kempf V, Wakamatsu K, Ito S, Simon J. 2004. Ion-exchange and adsorption of Fe(III) by *Sepia* melanin. *Pigment Cell Research* 17: 262–269.

Lubnow E. 1963. Melanine bei vögeln und säugetieren. *Journal für Ornithologie* 104: 69–81.

Lynch M, Ackerman MS, Gout J, Long H, Sung W, Thomas WK, Foster PL. 2016. Genetic drift, selection and the evolution of the mutation rate. *Nature Reviews Genetics* 17: 704–714.

Mackintosh JA. 2001. The antimicrobial properties of melanocytes, melanosomes, and melanin and the evolution of black skin. *Journal of Theoretical Biology* 211: 101–113.

Mateos-Gonzalez F, Senar JC. 2012. Melanin-based trait predicts individual exploratory behavior in siskins, *Carduelis spinus*. *Animal Behaviour* 83: 229–232.

McDonnel MJ, Pickett STA, Groffman P, Bohlen P, Pouyat RV, Zipperer WC, Parmelee RW, Carreiro MM, Medley K. 1997. Ecosystem processes along an urban–rural gradient. *Urban Ecosystems* 1: 21–36.

McDonnell MJ, Hahs AK, Breuste JH. 2009. *Ecology of Cities and Towns: A Comparative Approach*. Cambridge University Press.

McGraw KJ. 2003. Melanins, metals, and mate quality. *Oikos* 102: 402–406.

McGraw KJ. 2006. Mechanics of carotenoid-based coloration. Pages 243–294 in Hill G McGraw K, eds. *Bird Coloration*, vol. 1. Harvard University Press.

McPherson FJ, Chenoweth PJ. 2012. Mammalian sexual dimorphism. *Animal Reproduction Science* 131: 109–122.

Messmer TA. 2020. Humans, wildlife, and our environment: One health is the common link. *Human–Wildlife Conflicts* 14: 69.

Miles LS, Rivkin LR, Johnson MTJ, Munshi-South J, Verrelli BC. 2019. Gene flow and genetic drift in urban environments. *Molecular Ecology* 28: 4138–4151.

Mills LS, Zimova M, Oyler J, Running S, Abatzoglou JT, Lukacs PM. 2013. Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proceedings of the National Academy of Sciences* 110: 7360–7365.

Møller AP, Mousseau TA. 2001. Albinism and phenotype of barn swallows (*Hirundo rustica*) from Chernobyl. *Evolution* 55: 2097–2104.

Murray M, Cembrowski A, Latham AD, Lukasik VM, Pruss S, Clair St, CC. 2015. Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human–wildlife conflict. *Ecography* 38: 1235–1242.

Murray MH, Sánchez CA, Becker DJ, Byers KA, Worsley-Tonks KEL, Craft ME. 2019. City sicker? A meta-analysis of wildlife health and urbanization. *Frontiers in Ecology and the Environment* 17: 575–583.

Nachman MW, Hoekstra HE, D'Agostino SL. 2003. The genetic basis of adaptive melanism in pocket mice. *Proceedings of the National Academy of Sciences* 100: 5268–5273.

Niecke M, Heid M, Krüger A. 1999. Correlations between melanin pigmentation and element concentration in feathers of white-tailed eagles (*Haliaeetus albicilla*). *Journal für Ornithologie* 140: 355–362.

Niecke M, Rothlaender S, Roulin A. 2003. Why do melanin ornaments signal individual quality? Insights from metal element analysis of barn owl feathers. *Oecologia* 137: 159–158.

Niemelä J. 2011. *Urban Ecology: Patterns, Processes, and Applications*. Oxford University Press.

Noël S, Ouellet M, Galois P. 2007. Impact of urban fragmentation on the genetic structure of the eastern red-backed salamander. *Conservation Genetics* 8: 599–606.

Obukhova NY. 2007. Polymorphism and phene geography of the blue rock pigeon in Europe. *General Genetics* 43: 492–501.

O'Donnell K, delBarco-Trillo J. 2020. Changes in the home range sizes of terrestrial vertebrates in response to urban disturbance: A meta-analysis. *Journal of Urban Ecology* 6: juaa014.

Oke TR. 1973. City size and the urban heat island. *Atmospheric Environment* 7: 769–779.

MQR MQ, Ruxton GD. 2020. Camouflage in predators. *Biological Reviews* 95: 1325–1340.

Plum L, Rink L, Haase H. 2010. The essential toxin: Impact of zinc on human health. *International Journal of Environmental Research and Public Health* 7: 1342–1365.

Price TD. 2006. Phenotypic plasticity, sexual selection and the evolution of colour patterns. *Journal of Experimental Biology* 209: 2368–2376.

Prokop P, Randler C. 2018. Biological predispositions and individual differences in human attitudes toward animals. Pages 447–466 in Alves RRN Albuquerque UP, eds. *Ethnozoology: Animals in Our Lives*. Academic Press

Protas ME, Patel NH. 2008. Evolution of coloration patterns. *Annual Review of Cell and Developmental Biology* 24: 425–446.

Rainbow P. 2007. Trace metal bioaccumulation: Models, metabolic availability, and toxicity. *Environment International* 33: 576–582.

Randi E, Lucchini V. 2002. Detecting rare introgression of domestic dog genes into wild wolf *Canis lupus* populations by Bayesian admixture analyses of microsatellite variation. *Conservation Genetics* 3: 29–43.

Rivkin LR, et al. 2019. A roadmap for urban evolutionary ecology. *Evolutionary Applications* 12: 384–398.

Rosenblum EB, Römpler H, Schöneberg T, Hoekstra HE. 2010. Molecular and functional basis of phenotypic convergence in white lizards at White Sands. *Proceedings of the National Academy of Sciences* 107: 2113–2117.

Roulin A. 2004. The evolution, maintenance, and adaptive function of genetic colour polymorphism in birds. *Biological Reviews* 79: 815–848.

Sadoul B, Blumstein DT, Alfonso S, Geffroy B. 2021. Human protection drives the emergence of a new coping style in animals. *PLOS Biology* 19: e3001186.

Saunders NJ. 1998. *Icons of Power: Feline Symbolism in the America*. Routledge.

Schell CJ. 2018. Urban evolutionary ecology and the potential benefits of implementing genomics. *Journal of Heredity* 109: 138–151.

Schell CJ, Dyson K, Fuentes TL, Des Roches S, Harris NC, Miller DS, Woelfle-Erskine CA, Lambert MR. 2020. The ecological and evolutionary consequences of systemic racism in urban environments. *Science* 369: eaay4497.

Schell CJ, Stanton LA, Young JK, Angeloni LM, Lambert JE, Breck SW, Murray MH. 2021. The evolutionary consequences of human–wildlife conflict in cities. *Evolutionary Applications* 14: 178–197.

Schmutz SM, Berryere TG, Barta JL, Reddick KD, Schmutz JK. 2007. Agouti sequence polymorphisms in coyotes, wolves, and dogs suggest hybridization. *Journal of Heredity* 98: 351–355.

Senar JC, Conroy MJ, Quesada J, Mateos-Gonzalez F. 2014. *Ecology and Evolution* 4: 2625–2632.

Serieys LEK, Lea A, Pollinger JP, Riley SPD, Wayne RK. 2015. Disease and freeway drive genetic change in urban bobcat populations. *Evolutionary Applications* 8: 75–92.

Serieys LEK, et al. 2018. Urbanization and anticoagulant poisons promote immune dysfunction in bobcats. *Proceedings of the Royal Society B* 285: 20172533.

Service CN, Bourbonnais M, Adams MS, Henson L, Neasloss D, Picard C, Paquet PC, Darimont CT. 2020. Spatial patterns and rarity of the white-phased "spirit bear" allele reveal gaps in habitat protection. *Ecological Solutions and Evidence* e12014.

Sheshardri A, Borrus M, Yoder M, Robinson T. 2021. Midlatitude error growth in atmospheric GCMs: The role of eddy growth rate. *Geophysical Research Letters* 48: e2021GL096126.

Sih A, Ferrari MCO, Harris DJ. 2011. Evolution and behavioral responses to human-induced rapid environmental change. *Evolutionary Applications* 4: 367–387.

Skelhorn J, Rowe C. 2016. Cognition and the evolution of camouflage. *Proceedings of the Royal Society B* 283: 20152890.

Snoeijs T, Dauwe T, Pinxten R, Vandesande F, Eens M. 2004. Heavy metal exposure affects the humoral immune response in a free-living small songbird, the great tit (*Parus major*). *Archives of Environmental Contamination and Toxicology* 46: 399–404.

Somers CM, Yauk CL, White PA, Parfett CLJ, Quinn JS. 2002. Air pollution induces heritable DNA mutations. *Proceedings of the National Academy of Sciences* 99: 15904–15907.

Stencel JE, Ghent AW. 1987. Analyses of annual surveys of white and gray squirrels (*Sciurus carolinensis*) in Olney, Illinois, 1977–1986. *American Midland Naturalist* 118: 251–257.

Stevens M, Searle WTL, Seymour JE, Marshall KLA, Ruxton GD 2011. Motion dazzle and camouflage as distinct anti-predator defenses. *BMC Biology* 9: 1–11.

Stronen AV, et al. 2022. Wolf-dog admixture highlights the need for methodological standards and multidisciplinary cooperation for effective governance of wild x domestic hybrids. *Biological Conservation* 266: 109467.

Stuart-Fox D, Newton E, Clusella-Trullas S. 2017. Thermal consequences of colour and near-infrared reflectance. *Philosophical Transactions of the Royal Society B* 372: 20160345.

Suraci JP, Clinchy M, Zanette LY, Wilmers CC. 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters* 22: 1578–1586.

Szulkin M, Garroway CJ, Corsini M, Kotarba AZ, Dominoni D. 2020. How to quantify urbanization when testing for urban evolution? Pages 13–35 in Szulkin M, Munshi-South J Charmantier A, eds. *Urban Evolutionary Biology*. Oxford University Press.

Thirgood S, Woodroffe R, Rabinowitz A. 2005. The impact of human–wildlife conflict on human lives and livelihoods. Pages 13–26 in Woodroffe R, Thirgood S Rabinowtiz A, eds. *People and Wildlife: Conflict or Coexistence?* Cambridge University Press.

Todd NB. 1964. Gene frequencies of Boston's cats. *Heredity* 19: 47–51.

Todd NB. 1975. Gene frequencies in the cat population of New York City. *Heredity* 35: 172–183.

Troïanowski M, Dumet A, Condette C, Lengagne T, Mondy N. 2015. Traffic noise affects colouration but not calls in the European treefrog (*Hyla arborea*). *Behaviour* 152: 821–836.

Trust K, Miller M, Ringelman J, Orme I. 1990. Effects of ingested lead on antibody production in mallards (*Anas platyrhynchos*). *Journal of Wildlife Diseases* 26: 316–322.

Trut LN. 1999. Early canid domestication: The farm-fox experiment: Foxes bred for tamability in a 40-year experiment exhibit remarkable transformations that suggest an interplay between behavioral genetics and development. *American Journal of Science* 87: 160–169.

Tucker MA, Santini L, Carbone C, Mueller T. 2021. Mammal population densities at a global scale are higher in human-modified areas. *Ecography* 44: 1–13.

Turner MC, Andersen ZJ, Baccarelli A, Diver WR, Gapstur SM, Pope CA III, Prada D, Samet J, Thurston G, Cohen A. 2020. Outdoor air pollution and cancer: An overview of the current evidence and public health recommendations. *CA: A Cancer Journal for Clinicians* 70: 460–479.

van Grouw H. 2013. What color is that bird? The cause and recognition of common colour aberrations in birds. *British Birds* 106: 17–29.

van Grouw H. 2017. The dark side of birds: Melanism: Facts and fiction. *Bulletin of the British Ornithologists' Club* 137: 12–36.

van Grouw H, de Jong J. 2009. *Genetic bij Duiven: Modern Mednelisme en Meer Voor de Duivenliefhebber*. Nederlandse Bond van Sierduivenliefhebbersverenigingen.

Walsberg GE. 1983. Coat color and solar heat gain in animals. *BioScience* 33: 88–91.

Wayne RK, vonHoldt BM. 2012. Evolutionary genomics of dog domestication. *Mammalian Genome* 23: 3–18.

Wilkins AS, Wrangham RW, Fitch WT. 2014. The "domestication syndrome" in mammals: A unified explanation based on neural crest cell behavior and genetics. *Genetics* 197: 795–808.

Williams NSG, McDonnell MJ, Phelan GK, Keim LD, van der Ree R. 2006. Range expansion due to urbanization: Increased food resources attract grey-headed flying foxes (*Pteropus poliocephalus*) to Melbourne. *Austral Ecology* 31: 190–198.

Winchell KM, Reynolds RG, Prado-Irwin SR, Puente-Rolón AR, Revell LJ. 2016. Phenotypic shifts in urban areas in the tropical lizard *Anolis cristatellus*. *Evolution* 70: 1009–1022.

Wisconsin Department of Natural Resources. 1940. NR 10.02 Protected Wild Animals.Wisconsin Department of Natural Resources.

Wright S. 1945. The differential equation of the distribution of gene frequencies. *Proceedings of the National Academy of Sciences* 31: 382–389.

Xu X, et al. 2013. The genetic basis of white tigers. *Current Biology* 23: 1031–1035.

Yauk CL, Quinn JS. 1996. Multilocus DNA fingerprinting reveals high rate of genetic mutation in herring gulls nesting in an industrialized urban site. *Proceedings of the National Academy of Sciences* 93: 12137–12141.

Yauk CL, et al. 2008. Germ-line mutations, DNA damage, and global hypermethylation in mice exposed to particulate air pollution in an urban/industrial location. *Proceedings of the National Academy of Sciences* 105: 605–610.

Yeh PJ. 2004. Rapid evolution of a sexually selected trait following establishment in a novel habitat. *Evolution* 58: 166–174.

Zbyryt A, Mikula P, Ciach M, Morelli F, Tyrjanowski P. 2020. A large-scale survey of bird plumage colour aberrations reveals a collection bias in Internet-mined photographs. *International Journal of Avian Science 163:* 566–578.

Zhang MQ, Xu X, Luo SJ. 2014. The genetics of brown coat color and white spotting in domestic yaks (*Bos grunniens*). *Animal Genetics* 45: 652–659.

Zimova M, Mills LS, Nowak JJ. 2016. High fitness costs of climate change-induced camouflage mismatch. *Ecology Letters* 19: 299–307.