



Health as an outcome and driver of human–wildlife interactions

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Abstract

Human–wildlife interactions (HWIs) influence the health of humans and wildlife but a unifying framework is needed to understand the causes of HWIs to anticipate health-associated outcomes. In this article, we present a novel conceptual framework that positions wildlife and human health as outcomes of HWIs, human health risks and benefits as motivating factors to manage wildlife and HWIs, and wildlife and environmental health as drivers of future HWIs. We discuss policy implications, including centering wildlife health in preventing harmful HWIs and the wildlife health impacts of management actions to promote or prevent HWIs. We pose guiding questions for advancing health equity that explore who disproportionately experiences health risks and benefits arising from HWIs and who has the capacity to engage with management. Recognizing the integrated relationships between health and HWIs enables scientists and managers to collaboratively mitigate negative HWIs and promote favorable outcomes while protecting the health of people and wildlife.

Keywords: human–wildlife interactions, One Health, human–wildlife coexistence, public health, animal behavior

Human–wildlife interactions (HWIs) influence the health of people, wildlife, and the landscapes they share; a holistic understanding of the causes and outcomes of HWIs is critical for reducing harms and promoting coexistence. Alongside global urbanization and climate change (Abrahms et al. 2023, Newsom et al. 2023), HWIs—ranging from wildlife observations, property damage, and physical attacks—are increasing (Soulsbury and White 2019). The number of HWIs is expected to grow in the future because spatial overlap between people and wildlife is predicted to increase by over 40% by 2070 (Ma et al. 2024). Increases in HWIs, along with people's perceptions of wildlife as influenced by the media and community members, can determine the public's tolerance for wildlife and their support for habitat conservation, both of which are crucial for human–wildlife coexistence (Hathaway et al. 2017, Basak et al. 2022).

To better understand the root causes and diverse impacts of HWIs, we focus on health—of humans, animals, and ecosystems—as a driver and outcome of HWIs. To highlight the bidirectional relationships among health and HWIs, we present a novel conceptual framework with five key connections between HWIs and human, wildlife, and environmental health (figure 1). These five connections position wildlife and human health as outcomes of HWIs, human health risks and benefits as motivating

factors to manage wildlife and address concerns related to HWIs, and wildlife and environmental health as drivers of future HWIs. This health-centric focus can help identify factors that contribute to harms from HWIs and amplify favorable outcomes, for people and wildlife, that support coexistence. We define *coexistence*, following Pooley and colleagues (2021), as highly dynamic contexts wherein humans and wildlife share landscapes and where HWIs are managed such that wildlife can persist and where, although conflicts may occur, people accept tolerable levels of risk. We underscore that planning for coexistence requires an understanding of how HWIs affect the health of both people and wildlife (Carter and Linnell 2016, Frank et al. 2019). We use a One Health lens (figure 2), an integrated approach that optimizes the health of humans, animals, and the environment (Zinsstag et al. 2011), to focus on the diverse relationships between HWIs and human, animal, and ecosystem health.

Connection 1: Human–wildlife interactions affect human health

The first and best understood connection between HWIs and health is that HWIs affect human health (figure 1a). HWIs can promote human physical health through outdoor activities to

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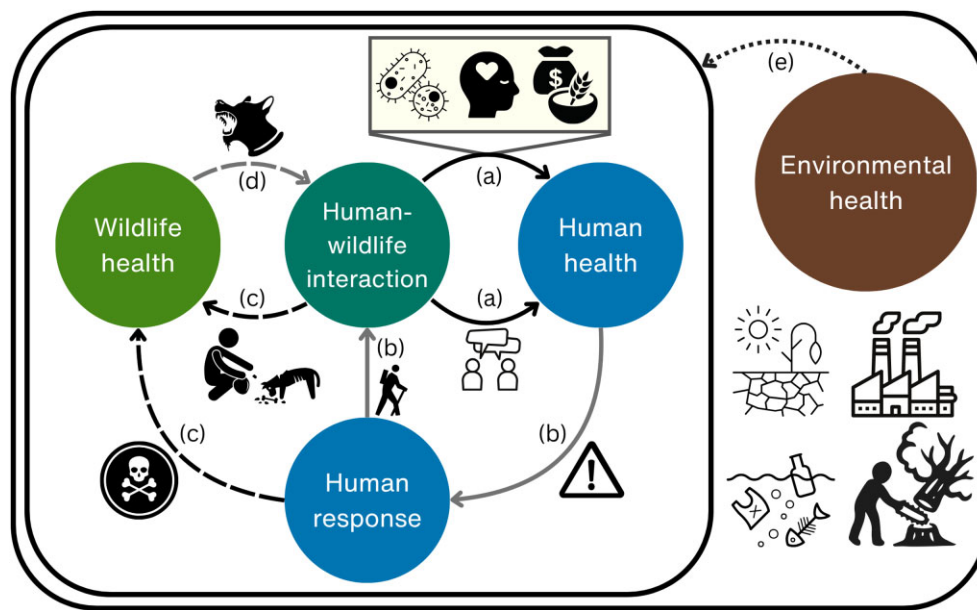


Figure 1. Conceptual framework showing the five key links and feedback loops among human–wildlife interactions (HWIs) and the health of humans, wildlife, and the environment. HWIs can affect human health either negatively or positively through direct encounters or conversations (a, the solid black arrows). Human health benefits and risks from wildlife can subsequently inform human responses to HWIs (b, the solid gray arrows), which may affect the likelihood of future HWIs (e.g., using or avoiding natural areas). Human actions to promote or prevent HWIs can then affect wildlife health either positively or negatively (c, dashed black arrows). Poor wildlife health can also influence the likelihood of future HWIs (d, the dashed gray arrow) if infections or other impairments cause behavioral changes in wildlife. All of these dynamics exist in the context of environmental health (e, the dotted black arrow) whereby resource availability influences the likelihood that humans and wildlife will compete for water, food, and space.

observe wildlife (Twohig-Bennett and Jones 2018) and can promote mental health via stress relief and mental restoration—for example, from hearing birdsong (Ferraro et al. 2020). Shared group experiences viewing wildlife can also promote social health (Rosales Chavez et al. 2023), and spiritual health through sightings of culturally important animals such as spotted hyenas (*Crocuta crocuta*) in Ethiopia (Young et al. 2020) or coyotes (*Canis latrans*) in desert communities (Larson et al. 2023). HWIs such as ecotourism-based wildlife viewing can promote economic opportunities that benefit human well-being (Das and Chatterjee 2015), especially when local people are involved in leadership roles (Khaledi Koure et al. 2023). Therefore, HWIs contribute to the physical, mental, social, and spiritual dimensions of human health (table 1) in myriad ways.

HWIs can also be detrimental to human health because they increase the risk of zoonotic diseases (Kruse et al. 2004) and economic losses (e.g., Barua et al. 2013), as well as injury and death (Bombieri et al. 2023). Zoonotic sources account for the majority of emerging infectious diseases in humans (Smith et al. 2014) and contribute to more than \$20 billion in direct costs (i.e., health-care) and over \$200 billion in indirect costs (i.e., economic damages) per decade (World Bank 2010). HWIs can also disrupt livelihoods and food security, including livestock depredation, crop raiding, and pathogen transmission from wildlife to livestock (Jadhav and Barua 2012, Barua et al. 2013, Clifford et al. 2013). HWIs can also lead to human injury. In the United States, more than a million insurance claims are filed annually following wildlife–vehicle collisions, and more than 47,000 people seek medical attention annually after wildlife attacks or bites (mostly by snakes, birds, rodents, and raccoons), although mortality associated with attacks is very rare (approximately 8 killed annually; Conover 2019). Hearing about or experiencing such events may trigger fear, anxiety, and other negative emotions that affect mental health (Galley and Anthony 2024). Even in less acute situations, milder

forms of stress exist, such as safeguarding pets and small children from predators (Keener-Eck et al. 2020, Larson et al. 2023) or hearing about predator attacks from neighbors or the media (figure 1a; Sabatier and Huveneers 2018). In response to such concerns, decisions about lethal management are often controversial and disagreements may affect the mental health of residents and managers involved in management decision-making (Epstein and Haggerty 2022). Furthermore, hunters and practitioners directly involved in culls and other forms of lethal management justified by human, animal, or environmental health may experience emotional discomfort and moral distress (von Essen and Redmalm 2024). Therefore, HWIs may be perceived as a stressor for human physical, mental, social, and spiritual health (table 1).

Connection 2: Human health drives responses to human–wildlife interactions

The human health risks and benefits described above, either perceived or realized, subsequently inform how wildlife are managed, either formally or informally. Therefore, the second connection in our framework positions human health risks and benefits as drivers of human responses to HWIs (figure 1b). In response to perceived health and safety risks and benefits, individuals may change their attitudes toward and tolerance for wildlife, affecting individual behaviors, support for management approaches including conservation activities, and interactions with wildlife and the outdoors. People who have had favorable experiences with wildlife may seek additional experiences to observe wildlife and may actively attract wildlife to their home. For example, enjoyment is a main motivator for feeding and watching birds (Cox and Gaston 2016, Randler and Großmann 2022), suggesting that the mental health benefits of HWIs can lead to human responses as feedback loops that promote additional HWIs. Conversely,

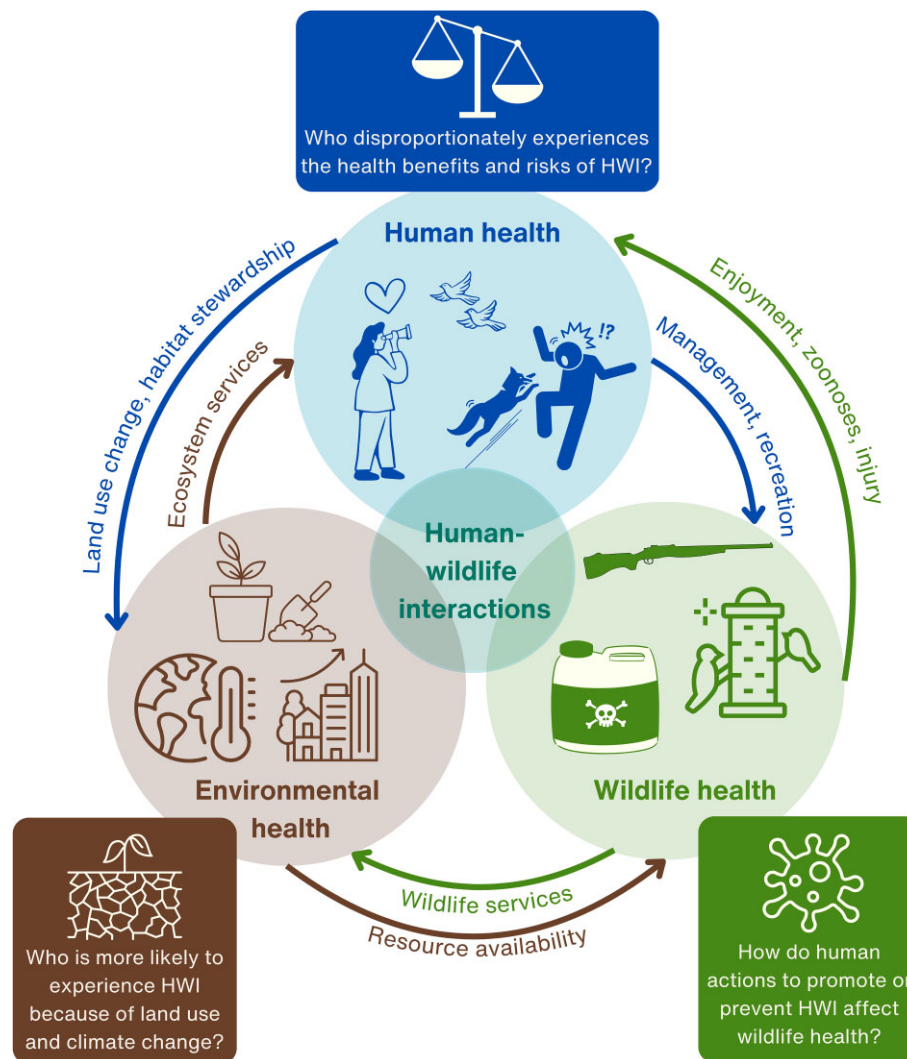


Figure 2. One Health diagram showing the links among human health, wildlife health, and environmental health in the context of human-wildlife interactions (HWIs; the arrows) as well as key guiding questions to advance health equity and human-wildlife coexistence (the boxes). The terms on the arrows are illustrative examples and not exhaustive.

people who perceive greater risk from wildlife may remove wildlife attractants from their property or use lethal management to kill or deter particular species (e.g., rodenticides; Morzillo and Mertig 2011a). Individuals may also change how they interact with nature—for example, avoiding hiking off trail due to concerns about Lyme disease (Nategh and Chen 2021). In this way, human health risks and benefits can inform future human actions and feedback loops that relate to behaviors affecting the likelihood of future HWIs.

Health concerns stemming from HWIs also shape management decisions, particularly lethal management. Culling and selective killing are common strategies for disease control in response to biosecurity concerns related to human health, as well as the health of other domestic and wild animals (Degeling et al. 2016). Concerns about disease can rapidly and dramatically change human-wildlife relations and the politics of management (Broz et al. 2021). For example, emerging concerns about the transmission of African swine fever from wild boar to domestic pigs have motivated the culling of wild boar in Europe (von Essen et al. 2023). Similarly, many species around the world have been culled to prevent the transmission of *Mycobacterium bovis*, the causative agent of bovine tuberculosis, to cattle including European bad-

gers (*Meles meles*) in the United Kingdom and the Republic of Ireland, brushtail possums (*Trichosurus vulpecula*) in New Zealand, and African buffalo (*Syncerus caffer*) with mixed efficacy (Miguel et al. 2020). The expansion of deer hunting and culling in suburbs in the United States is often initiated by concerns about the role deer play in the transmission of Lyme disease (Kugeler et al. 2016) and wildlife-vehicle collisions (Conover 2019). Outside of urban areas, lethal management is one of the main methods to control the spread of chronic wasting disease, a fatal prion disease, in wild ungulates out of concerns for the health of the animals and the people who consume them (Uehlinger et al. 2016). Therefore, human perception of HWIs influences management actions affecting diverse facets of wildlife health.

Connection 3: Wildlife health is influenced by human-wildlife interactions and their management

The actions to attract, repel, or depopulate wildlife described above can subsequently affect wildlife health. Therefore, the third connection focuses on wildlife health as an outcome of human actions to promote or prevent HWIs (figure 1c). One of the most

Table 1. Dimensions of human, animal, and environmental health and their associated health benefits and harms from HWIs.

Category	Dimension	Definition	Relevance to HWIs
Human health	Physical	The ability to perform daily activities, maintain bodily functions, and prevent diseases (Pate 1988).	Harmed by attacks (Conover 2019), promoted by wildlife-centric outdoor activities (Rosales Chavez et al. 2023).
	Mental	Emotional, psychological, and social well-being, influencing how individuals think, feel, and act in their daily interactions and in response to stressors (Layard 2013).	Harmed by anxiety about crop raiding (Galley and Anthony, 2024), promoted by hearing bird song (Ferraro et al. 2020).
	Social	The ability of individuals to form satisfying interpersonal relationships and adapt to social situations, including the impact of socioeconomic status and community support on an individual's vulnerability to disease (Tarlov, 2002).	Harmed by disagreements about wildlife management (Epstein and Haggerty 2022), promoted by communal experiences in nature (Rosales Chavez et al. 2023).
	Spiritual	A high level of hope, and commitment to a well-defined worldview or belief system, which provides a sense of meaning and purpose in life and offers an ethical path to personal fulfillment, and connectedness to oneself and others (Dhar et al. 2011).	Promoted by encountering culturally and spiritually important animals (e.g., hyenas, Baynes-Rock 2015).
Animal health	Biological traits	Genetic and physiologic indicators of health including growth, disease, body condition, stress, and reproductive success (Wittrock et al. 2019).	Harmed and promoted by supplemental feeding (Box 1).
	Social environment	Ability for an animal to express typical social behaviors, affected by factors such as population dynamics, abundance, and demographic structure (Wittrock et al. 2019).	Harmed by culling in response to negatively perceived HWIs or health risks (Shannon et al. 2013).
	Needs for daily living	Ability to access adequate nutrition through factors such as habitat quality and food availability (Wittrock et al. 2019).	Promoted by habitat stewardship (Mumaw and Mata 2022).
Environmental health	Ecosystem functioning	Ability of an ecosystem to maintain function in times of stress (Müller et al. 2020).	Harmed by rodenticide use (Nakayama et al. 2019).
	Ecosystem services	Provisioning ecosystem services that contribute to human and animal health (Müller et al. 2020).	Harmed by land use change to prevent HWIs (e.g., draining wetlands to prevent mosquito bites, Dale and Knight 2008)

common ways for people to promote HWIs is by feeding wildlife (i.e., food provisioning). Food provisioning promotes the risk of human-wildlife and inter- and intraspecies pathogen transmission by increasing local wildlife densities, increasing contact rates between potential disease hosts (for a review, see Becker et al. 2015, Murray et al. 2016). Local aggregations of animals also might contaminate areas with environmentally persistent pathogens (Murray et al. 2021a). Food provided to wildlife by people, intentionally or otherwise, may be beneficial or detrimental depending on nutritional content, affecting body condition (Wilcoxon et al. 2015), immune function (Strandin et al. 2018), and reproductive output (Plummer et al. 2013). Increased contact between wildlife and humans from hand feeding also may contribute to anxiety-related behaviors in wildlife (Maréchal et al. 2011). Particular species are disproportionately more likely to consume human-provided foods on the basis of diet or other behaviors (Galbraith et al. 2017), potentially altering disease ecology dynamics at the wildlife community level. Because of this complexity, knowledge about food quality, pathogen transmission mode, and host communities are necessary to anticipate health outcomes of food provisioning (box 1).

Human actions to prevent future HWIs can also affect wildlife health. One of the most common types of negatively perceived HWIs is infestations of commensal rodents (e.g., black rats

Rattus rattus, brown rats *Rattus norvegicus*, house mice *Mus musculus*) because they are prolific zoonotic hosts (Himsworth et al. 2013). One of the most common ways to manage commensal rats is bait containing anticoagulant rodenticides (Jacob and Buckle 2018), which cause acute illness and death in predators, particularly raptors (Nakayama et al. 2019). Exposure to anticoagulant rodenticides has also been associated with immune dysfunction and notoedric mange in wild felids (Riley et al. 2007, Serieys et al. 2018) and in San Joaquin kit foxes (Cypher et al. 2017), causing mortality and population declines. In rats, exposure to anticoagulants in surviving rats has been associated with increased prevalence of *Leptospira interrogans*, the causative agent of zoonotic leptospirosis (Murray and Sánchez 2021). Lethal removal of individual animals can also promote dispersal, increasing the risk of pathogen transmission among animals and spillover to people. For example, the prevalence of *Leptospira interrogans* increased following a rat trapping effort in Vancouver, likely because culling created opportunities for new rats to move in from adjacent city blocks (Lee et al. 2018). At a larger scale, culling to reduce local flying fox (*Pteropus* sp.) populations may also promote admixing between populations, and therefore pathogen transmission, because these bats can rapidly recolonize areas hundreds of kilometers away (Roberts et al. 2012). Knowledge of unintentional and secondary impacts on wildlife physiology and

Box 1. Supplemental feeding influences health trade-offs for humans and wildlife across scales.

Maintaining bird feeders is one of the most popular human actions to promote human–wildlife interactions (Reynolds et al. 2017) and creates health trade-offs for people and wildlife across ecological scales. Because feeders promote higher densities of birds and contact between humans and bird droppings, bird feeders can promote the transmission of pathogens between birds and people (figure 3a). For example, a multistate human salmonellosis outbreak in the United States resulted from handling sick and dead birds or contact with contaminated bird feeders (Patel et al. 2023). Individual birds that forage at feeders can have higher body condition and more rapid feather growth (figure 3b; Wilcoxon et al. 2015) but time spent at feeders is the strongest predictor of risk of mycoplasmal conjunctivitis in house finches (figure 3c; Adelman et al. 2015). At the population level, bird feeding is associated with earlier laying dates, which is often beneficial for young (figure 3d; Robb et al. 2008), but feeders are also associated with higher rates of intra- and interspecific aggression (figure 3e; Wojczulanis-Jakubas et al. 2015). At the community scale, feeders preferentially benefit particular species and individuals, altering avian community structure (figure 3f; Galbraith et al. 2017, Plummer et al. 2019), which could affect pathogen dynamics if feeding promotes species that are more or less likely to transmit pathogens (i.e., the dilution effect; Keesing and Ostfeld 2021). Feeders also attract nontarget mammals such as squirrels and raccoons, facilitating the spread of generalist pathogens (figure 3g; Reed and Bonter 2018). For humans, individuals who maintain a feeder and watch birds reported increased feelings of relaxation (figure 3h; Cox and Gaston 2016) but nearly half of bird feeders reported they would feel sad if they saw diseased birds at their feeder (figure 3i; Dayer et al. 2019). Within neighborhoods, survey respondents expressed a duty to maintain neighborhood standards when it comes to wildlife-friendly gardening, suggesting that local interest in supporting birds could lead to the diffusion of wildlife-friendly actions (figure 3j; Goddard et al. 2013). Conversely, feeding birds can lead to social conflict between neighbors because bird feeders can attract unpopular mammals such as rats (figure 3k; Reed and Bonter 2018). At the city scale, the popularity of feeding birds may affect local opportunities for recreational birdwatching because young adults who feed birds were motivated by sharing their sightings with others and participating in citizen or community science projects (figure 3l; Martin and Greig 2019). More opportunities for recreational birdwatching is beneficial for public health because it is associated with psychological restoration (Randler and Großmann 2022) and greater cognitive maintenance and mobility in nursing homes (Zieris et al. 2023). Conversely, public health concerns may arise in cities where feeding birds such as pigeons in parks and public squares is common because pigeons can shed antimicrobial resistant pathogens in their droppings (figure 3m; Wilson et al. 2024). The many health impacts of bird feeding for humans and wildlife across scales demonstrate that it is difficult to determine a net health effect of HWIs. Rather, understanding health trade-offs can help advance messaging and policy to promote health benefits and mitigate health harms.

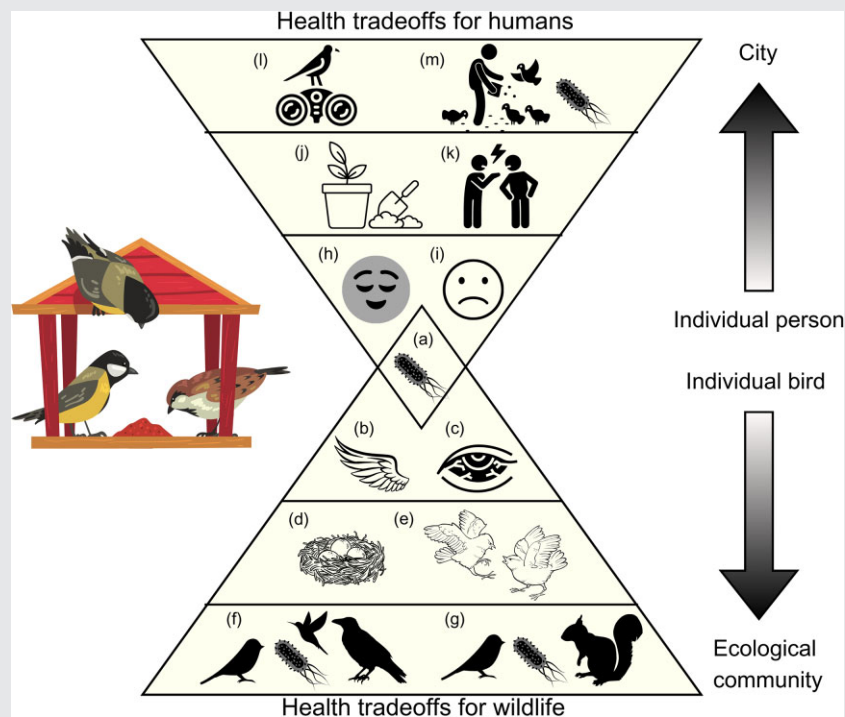


Figure 3. Health trade-offs associated with supplemental feeding for people and wildlife across ecological scales.

behavior are therefore important when selecting management strategies.

Connection 4: Wildlife health drives human–wildlife interactions

Changes in wildlife health subsequently affect animal behavior. Therefore, the fourth connection focuses on wildlife health as a driver of future HWIs (figure 1d). Unhealthy animals in human-dominated areas contend with increased energy demands to maintain homeostasis and decreased ability to obtain resources. These challenges, when combined with anthropogenic disturbance, affects the likelihood of risky behavior with respect to humans. For example, mountain lions (*Puma concolor*) avoid human settlements less if they are more desperate to find prey (Blecha et al. 2018). Animals with poor body condition are more likely to forage near human settlements such as farms (e.g., pumas, Luque-Machaca et al. 2023; tapirs *Tapirus bairdii*; Pérez Flores et al. 2020; Asiatic lions *Panthera leo persica*; Vijayan and Pati 2002) or near houses (polar bears *Ursus maritimus*; Towns et al. 2009). Therefore, HWIs are more likely when and where unhealthy animals have unmet resource demands that may lead to risk-prone behaviors.

Some neurological diseases contribute to wildlife behaviors that lead animals to act differently toward people, such as increased aggression and decreased wariness. Neurologic diseases such as rabies and canine distemper virus cause infected animals to stagger toward people with teeth bared, eliciting the moniker of “zombie raccoons” (Richards et al. 2008). Encephalitis from neurologic diseases is also an increasingly recognized cause of HWIs in black bears (*Ursus americanus*) that exhibit reduced wariness toward humans (Sinnott et al. 2022). Similarly, mule deer (*Odocoileus hemionus*) with late-stage chronic wasting disease were more susceptible than uninfected deer to vehicle-related mortality likely because advanced disease leads to loss of muscle coordination and cognition, reducing the ability of diseased deer to recognize and avoid vehicles (Krumm et al. 2005). Therefore, mitigating health risks for wildlife may also prevent harmful HWIs for both people and wildlife.

Connection 5: Environmental health influences human–wildlife interactions

HWIs must always be considered within the context of the habitat in which they occur, which determines resource availability and environmental health harms such as pathogens or toxicants. As such, the fifth connection between health and HWIs positions environmental health as a driver of future HWIs (figure 1e). One of the most influential processes affecting environmental health is land use change, such as the conversion of forests, grasslands, and wetlands to urban or agricultural land, which increases human–wildlife overlap and opportunities for pathogen spillover (Plowright et al. 2021). Residents in Bangladesh reported that rhesus macaques (*Macaca mulatta*), which host several zoonotic viruses, were more dependent on backyard fruit trees and human-associated water sources after construction projects altered nearby forested land and filled in rivers (Shano et al. 2021). In a scoping review, White and Razgour (2020) described several examples of how land use change promotes HWIs, including contact between people and urban-adapted hosts (e.g., rodents) with urbanization, increased contact among people, bats, and primates after deforestation and concurrent removal of foraging habitat, agricultural intensification influencing the transmission of diseases associated with livestock, and habitat fragmenta-

tion affecting host community structure and contact with generalist vectors. Taken together, land use change typically facilitates contact between people and species that are able to exploit alternative habitats (e.g., macaques, rodents) or are displaced from foraging areas (e.g., fruit bats).

Environmental health is also affected by climate change, which can influence HWIs by altering resource availability as well as the behavior of people and wildlife (for a review, see Abrahms et al. 2023). Climate change may affect resource availability through droughts, fires, and floods, which may result in reduced resource availability for wildlife. For example, rates of human–bear conflicts are higher in drought years with low fruit production (Parchizadeh et al. 2023). In Tanzania, elephants (*Loxodonta* sp.) are more likely to raid crops during times of drought, and villagers therefore are less tolerant of elephant encounters due to resulting food insecurity because of destroyed crops and pipes, which may lead to retaliatory elephant killing (Mariki et al. 2015). Changing seasonal patterns in temperature and precipitation have also led to shifts in the geographic distribution of disease vectors such as mosquitos (Carlson et al. 2023) and ticks (Gray et al. 2009). This creates new opportunities for host–vector contact for both people and animals, including in cities due to the urban heat island effect (LaDeau et al. 2015). In combination, climate change increases overlap between people and wildlife, novel host–vector–pathogen contacts, and food and economic insecurity for people, thereby enhancing the other four framework connections in different ways depending on the species and location. Growing support for One Health approaches to such problems can help predict and disentangle these changes. As an example of this interconnectedness, rising ocean temperatures have led to more frequent red tide algal blooms, which can cause respiratory problems in people (Grattan et al. 2016) and produce domoic acid, a neurotoxin (Horner et al. 1997), which bioaccumulates and leads to aggression in California sea lions (*Zalophus californianus*) toward people (Goldstein et al. 2008). These connections between climate change, human health, wildlife health, and HWIs will become increasingly important as climate-related disruptions become more frequent and severe.

Feedback loops among health and HWIs

The examples above support the framework connections between HWIs and human health risks or benefits, the actions people take in response to those risks or benefits, subsequent impacts on wildlife health and behaviors relevant to HWIs, and the role of environmental health in creating contexts that influence the rates and outcomes of HWIs. Taken together, these connections create a feedback loop that can exacerbate harmful HWIs or lead to coexistence. For example, concerns about zoonotic disease risk from commensal rat infestations often leads to the use of anticoagulant rodenticides to kill rats (Jacob and Buckle 2018), which can subsequently increase the susceptibility of carnivores to diseases such as mange (Riley et al. 2007, Serieys et al. 2018). Notedric and sarcoptic mange cause hair loss and lesions, leading to increased energy demands (Cross et al. 2016) and secondary infections. These physiological changes may explain why carnivores with mange are more likely to eat human-associated foods (e.g., coyotes; Murray et al. 2015a, 2015b). Potentially to access easily accessible resources, carnivores with mange are also more likely to be detected near human settlements and in more urbanized areas (e.g., black bears, Fitzgerald et al. 2008; gray wolves *Canis lupus*, Shelley and Gehring 2002, Jimenez et al. 2010; raccoon dogs *Nyctereutes procyonoides*, Saito and Sonoda 2017; coyotes, Murray et al. 2015a, 2021b, Reddell et al. 2021; mountain lions, Riley

Box 2. P22, the lion of Los Angeles, as a case study in carnivore health and coexistence.



Figure 4. Mountain lion P22 with signs of notoedric mange (a) and after he recovered (b). Photos were taken during capture (a) and using remote wildlife cameras (b) in Los Angeles, California, in the United States.

Urban large carnivores pose unique challenges for human–wildlife coexistence because of their large home ranges, demanding prey requirements, and safety concerns for people and domestic animals. However, high-profile individuals such as the mountain lion (a.k.a. cougar) known as P22 in Los Angeles highlight the potential for coexistence. P22 is an unusual case of a large obligate carnivore persisting in a park within Los Angeles, the second largest metropolitan area in the United States (greater than 18 million residents; US Census Bureau 2025). National Park Service scientists began tracking P22's movements as a subadult in 2012 using a GPS collar and motion-triggered wildlife cameras (Riley et al. 2021). P22 typically stayed within Los Angeles's Griffith Park; only 2% of his locations were in urban areas between March 2012–December 2013 (Sikich and Riley 2014). In early 2014, wildlife camera photos revealed that P22 had lesions, crusts, and hair loss consistent with notoedric mange (figure 4a). P22 was recaptured in March 2014 to replace his GPS collar, treat the mange, and collect a blood sample. P22's blood tested positive for anticoagulant rodenticides, which have been associated with mange in bobcats (Riley et al. 2007). In the four months prior to recapture, when P22 was photographed with signs of mange, 37% of P22's locations were in urban areas, showing a dramatic increase in urban land use during mange infestation (Sikich and Riley 2014). Several months later, P22 appeared to have recovered from mange on the basis of wildlife camera detections (figure 4b) and his land cover use returned to the pattern prior to the mange infestation.

P22 had very few direct encounters with people or pets until 2022. In late 2022, his landscape use shifted again to 24% of locations in urban areas, up from 7% the year prior. In November–December 2022, P22 attacked three leashed dogs, killing one and injuring two, and injured two of the owners as they intervened, necessitating management intervention (Gammon 2022). P22 was recaptured on December 12, 2022 and had demodectic mange, systemic ringworm, an orbital fracture from a recent vehicle collision, and a severe hernia (NPS 2023). In light of his advanced age, health issues, and conflicts, the California Department of Fish and Wildlife decided on euthanasia, in consultation with other agencies.

This chronology highlights the relationship between P22's health and behavior. Over the 10 years that he was monitored, P22 lived entirely within the Griffith Park area, preyed on species-typical prey such as deer, coyotes and raccoons, and never approached people. These patterns changed in 2014 and 2022 when he was in poor health from mange and other causes. During these periods, P22 made greater use of urban areas, and in 2022 began attacking leashed dogs accompanied by people.

P22's general avoidance of residential areas facilitated coexistence with people, but public perceptions went beyond tolerance. In 2013, P22 achieved global fame after iconic images of him in front of the Hollywood sign were published by National Geographic. P22 was celebrated as an ambassador for resilience in an urbanizing world, due in part to outreach campaigns such as the National Wildlife Federation's SaveLACougars campaign. This legacy contributed to the creation of the Wallis–Annenberg road crossing structure to enhance landscape connectivity for cougars and other wildlife (Wilkinson 2023). Following P22's death, a celebration of life was held featuring stories from schoolchildren and celebrities about P22 strengthening their connection to the natural world. In summary, P22's story exemplifies the connections among wildlife health and HWIs, HWIs and human physical and mental health, and how people and carnivores can coexist even in large cities. Photograph: National Park Service.

et al. 2007; see box 2). As a result of shifts in diet and habitat use, carnivores with mange can be disproportionately more likely to be reported as nuisance animals (Murray et al. 2015b), increasing rates of negatively perceived HWIs. This cycle between realized and perceived health risks from rodents (figure 1a), actions to prevent those risks (figure 1b), subsequent changes for carnivore health and behavior (figure 1c), and likelihood of

future human–carnivore interactions (figure 1d) may be further exacerbated by environmental conditions conducive to pests, such as urban intensification and milder winters associated with climate change (figure 1e).

As a more favorable example, perceived health benefits from bird watching such as peace and relaxation can motivate people to engage in wildlife-friendly gardening to attract birds to their

yard (Goddard et al. 2013). Birds with more access to high-quality forage, such as caterpillars for their young, have better body condition and reproductive outcomes, leading to greater bird abundance and diversity (Seress et al. 2018) and therefore opportunities for residents to benefit further from bird watching. This virtuous cycle is supported by environmental conditions conducive to birds and caterpillars such as plant diversity and canopy cover in the neighborhood, which is, in part, dictated by current socioeconomic characteristics and land use legacies (Riley and Gardiner 2020; see the “Implications for environmental justice and health equity” section below). These two scenarios demonstrate the importance of integrated relationships between human and wildlife health and environmental change in anticipating future HWIs.

Context dependence

The net outcomes of these feedback loops for human and wildlife health are dependent on human, wildlife, and environmental contexts. The impact of HWIs on human mental health is substantially mediated by public perceptions of and affective responses to wildlife, which are influenced by situational factors, people's past experiences, and sociocultural factors. Situational factors that affect HWIs and associated outcomes include physical distance between animals and people and the location of encounters. For instance, in Arizona, people were more likely to support or take lethal action if snakes—especially venomous ones—are in people's homes or if children are present (Larson et al. 2023). Previous experiences with wildlife also influence people's attitudinal and behavioral responses and associated outcomes; for example, individuals who are accustomed to seeing wildlife such as snakes and coyotes and have had safe encounters may feel favorably toward or more comfortable around them (Haight et al. 2023). But people who experience acute or chronic threats that result in personal or economic harm may be more fearful or they may experience emotional and financial distress from HWIs, thereby exacerbating conflicts and impaired health for people as well as wildlife (e.g., through lethal control of problem animals; Mariki et al. 2015). Finally, sociocultural factors mediate people's responses to HWIs through socialization that results in shared beliefs (e.g., norms and traditions), as well as religious beliefs or superstitions about particular animals. Bats are often viewed as evil and are associated with devils and witchcraft in Western culture but are viewed more favorably among Asia-Pacific cultures (Low et al. 2021). Furthermore, spotted hyenas are appreciated as spiritual protection against harmful spirits by Harar residents in Ethiopia (Baynes-Rock 2015). Ethiopia is one of the world's most populated countries, but spotted hyenas live in many urban areas in ways that can be considered coexistence (Young et al. 2020) given that people tolerate occasional hyena attacks on humans (Baynes-Rock 2015). Therefore, understanding HWIs in the context of individual experience, location, and related cultural norms and practices is important for understanding feedback loops in our framework.

The human health risks and benefits associated with HWIs also depend on the wildlife species involved and their capacity to harm or benefit people. Wildlife traits including size, diet, and associated behaviors affect HWIs and how people respond to particular taxa or species. Species that more commonly raid crops (large herbivores, rodents), prey on livestock (large carnivores), or have the capacity to injure and kill people compound negative HWIs. For example, elephants cause intense damage from crop

raiding and are also the most common species causing human mortalities around reserves in India (Gulati et al. 2021) and in Nepal (Acharya et al. 2016). Importantly, the outcome of carnivore attacks varies by species, location, and context. For example, most of the fatal wildlife attacks reported in North America involved bears, whereas those causing nonfatal injuries were associated with other terrestrial carnivores (Garrote et al. 2017). Meanwhile, attacks on people by leopards and tigers in Nepal are similarly common but occur outside and inside of protected areas, respectively (Acharya et al. 2016). Whether the drivers of such attacks are due to human-wildlife overlap or human activities that elicit problem behaviors (e.g., tourists approaching wildlife) varies across contexts (Penteriani et al. 2016).

Despite these risks, predators can benefit human health (O'Bryan et al. 2018). Carnivores can reduce the likelihood of HWIs with zoonotic reservoirs such as rodents (Ostfeld and Holdt 2004), wild boar (*Sus scrofa*) (Tanner et al. 2019), and feral dogs (Braczkowski et al. 2018) by regulating prey populations. By reducing prey abundance, carnivores can also benefit human safety and livelihoods—for example, reducing vehicle collisions with deer (Gilbert et al. 2017) and crop raiding (e.g., dingoes consuming red kangaroo in Australia; Prowse et al. 2015). Therefore, the net impact of HWIs for human health depends on the relative risks and benefits posed by species occupying different niches within the ecological community.

Similarly, scavenging species also provide ecological services that can benefit human health. Avian and mammalian scavengers such as spotted hyenas, golden jackals (*Canis aureus*), and vultures (*Gyps* spp., *Neophron percnopterus*) consume wildlife and livestock carcasses, thereby reducing pathogen load in the environment (Gangoso et al. 2013, Ćirović et al. 2016, Sonawane et al. 2021). However, in the context of Old World vultures, scavenging on livestock has led to dramatic population declines and a One Health conservation crisis because of pharmaceuticals in the environment (Ottinger et al. 2021, Bean et al. 2024). In India and Pakistan, treating domestic cows with the anti-inflammatory drug diclofenac accidentally led to large-scale poisoning of vultures and rapid population declines starting in the 1990s (Green et al. 2004). In parts of Africa, vultures are poisoned unintentionally when farmers treat carcasses with diclofenac to poison carnivores in retaliation following livestock predation events (Ogada et al. 2012). Vultures are also poisoned intentionally by poachers using diclofenac because vulture circling can reveal poaching sites (Ogada et al. 2016). Vultures are therefore poisoned by pharmaceuticals used in response to domestic animal health concerns, HWIs that affect human livelihoods (livestock depredation), and HWIs that harms wildlife health (poaching), demonstrating the conservation implications of the connections between One Health and HWIs.

The connection between environmental health and HWIs is also context dependent. Rates of change in land use and climate are unequally distributed and their associated harms and benefits from HWIs will be disproportionately felt in specific locales. For example, spatial overlap between humans and wildlife is expected to increase on approximately two-thirds of land in Africa (70%) and South America (67%) but only approximately a third of land in North America (38%; Ma et al. 2024). Simultaneously, Africa is expected to disproportionately experience droughts exacerbated by climate change, which will likely also increase HWIs such as crop raiding (Mariki et al. 2015). Therefore, location-based impacts may require different responses to address feedback loops among human health, wildlife health, and HWIs.

Another aspect of context dependence is the categorization of HWIs as positive or negative. Whether the outcomes of HWIs are positive or negative depends on health metric, individual person, animal species, and time point under consideration. Instead, it is helpful to think about health trade-offs within individuals (i.e., different health metrics), among humans and wildlife (e.g., beneficial for one and detrimental for the other), and among different human communities or wildlife species (box 1). These trade-offs are also dynamic. Centering health in the life cycle of an interaction (Harris et al. 2023), HWIs that start as neutral can become beneficial for wildlife health and harmful for human health if an animal obtains a needed resource at the expense of human mental health and livelihood (e.g., crop raiding), which can then become negative for wildlife health if retaliatory action—such as lethal management—is taken. Conversely, interactions that begin as beneficial to wildlife physical health and human mental health (e.g., food provisioning) can become negative for both wildlife and people if it promotes the transmission of zoonotic pathogens among individuals and species. Therefore, we encourage research and management to focus on adapting to context-specific situations on the basis of current knowledge and ongoing assessments of the potential for different interactions and outcomes that might occur throughout the life cycle of HWIs.

Advancing policy by addressing feedback loops among health and HWIs

We encourage policies that address the integrated connections among health and HWIs (table 2). Specifically, policies might explicitly incorporate interdisciplinary approaches to health in wildlife management plans that consider how protecting wildlife health as central to preventing harmful HWIs, human actions to promote or prevent HWIs affects wildlife health for both target and nontarget species, and health risks and benefits from HWIs are communicated to the public to avoid undesirable actions toward wildlife.

The associations between poor wildlife health, behavior, and HWIs signals that preventing wildlife health risks are central in understanding the complexities of HWIs. As such, protecting wildlife health ultimately benefits human health, safety, food security, and economic stability. This connection creates a shared goal for veterinarians, disease ecologists, and managers that handle HWIs such as wildlife damage officers, animal control officers, and government agencies involved in HWIs perceived harmful to people (e.g., USDA Wildlife Services). Importantly, this perspective shift moves wildlife disease from a natural form of population control not requiring intervention (i.e., letting nature take its course) to a phenomenon that may result in increased HWIs and may have been exacerbated by human actions. Such a shift encourages emphasis to anticipating increased HWIs during some types of wildlife disease outbreaks or epizootics, to examining patterns in disease cases to identify any human-associated drivers of pathogen transmission or toxicity, and to increased collaboration between wildlife health agencies and animal control or damage management entities. All three of these areas require a proactive approach that acknowledges the interconnectedness of wildlife health, behavior, and human actions toward wildlife.

To effectively center wildlife health in the management of HWIs, policy must consider how human actions to promote or prevent HWIs affect different aspects of wildlife health. For example, humans intentionally provide hundreds of pounds of food

for wildlife via hand feeding or feeding stations to attract wildlife for recreation, hunting, management, and ecotourism (Cox and Gaston 2018, Balasubramaniam et al. 2022). Bird feeding is the most widespread source of food provisioning; between 27% and 48% of households feed birds, depending on their location (Davies et al. 2009, Brandtner 2023). Backyard feeding of mammals is less frequent (e.g., 7%–12% of households deliberately feeding foxes in the United Kingdom; Baker et al. 2004). Motivations for feeding backyard wildlife include a desire to help animals (Clark et al. 2019), connecting with nature, better viewing opportunities (Baker et al. 2004), and religious beliefs (Sengupta and Radhakrishna 2020). Stronger regulations and enforcement to limit supplemental feeding are important to prevent wildlife disease outbreaks; however, the commonness of food provisioning, as well as the diverse motivations for feeding means that efforts to restrict supplemental feeding could include opportunities to offer alternative ways to connect with nature. To help mitigate negative impacts of food provisioning for wildlife health, researchers can identify contexts that are particularly problematic for wildlife health (e.g., during outbreaks, low quality food, feeder hygiene) on the basis of public motivation to help animals.

Wildlife managers are empowered to proactively anticipate how human actions to promote or prevent HWIs will affect wildlife health, because changes in wildlife health may influence rates of future HWIs. The alternative, reactive approach may create epizootics that lead to greater harm to both humans and wildlife while potentially disrupting ecosystem dynamics and exacerbating human–wildlife and human–human conflicts. For example, using anticoagulant rodenticides to manage commensal rodents in response to disease concerns can lead to lose–lose outcomes for human and wildlife health from nontarget poisoning in children, pets, and predators (Soleng et al. 2022). A more proactive approach would acknowledge that commensal rodents thrive in urban environments because of human-associated resources and invest instead in healthier communities through improved waste management and rodent-proof infrastructure (Lee et al. 2022). Proactive approaches that involve human behavior (e.g., attractant management) tend to be more effective; however, they are unfortunately studied less often (Morzillo and Schwartz 2011, Artelle et al. 2024). Proactive approaches are better able to be adaptive given the complex interrelationships between people, individual animals, wildlife populations, and ecosystems, which are often difficult to predict given uncertainties associated with global environmental change.

These human actions with respect to wildlife arise in part because of human perceptions of health risks and benefits. Therefore, thoughtful consideration is needed about how health risks and benefits are communicated to the public because communication can influence public attitudes and actions toward wildlife. The COVID-19 pandemic has demonstrated far-reaching outcomes of zoonotic disease concerns related to public attitudes toward wildlife and wildlife management. In China, people expressed more unfavorable attitudes about bats after the COVID-19 pandemic; unfavorable attitudes toward bats were associated with more support of bat culls and less support of protecting bat populations (Lu et al. 2021). In terms of actions that affect wildlife health, people are more likely to use rodenticides if they perceive more health risks from rodents (Morzillo and Mertig 2011a) but lack awareness of related environmental impacts (Morzillo and Schwartz 2011). However, behavioral intentions to use rodenticides could change on the basis of information about nontarget wildlife health impacts (Morzillo and Mertig 2011b) because many users lack understanding about product toxicity and appropriate

Table 2. Examples of common types of human–wildlife interactions (HWIs) and their relevance to human, wildlife, and environmental health, as well as policy recommendations to promote health benefits and reduce health harms.

Type of HWIs	Relevance to human health	Relevance to wildlife health	Relevance to environmental health	Policy implications
Crop raiding	Livelihood damages, anxiety, sleep loss, poor diet (Galley and Anthony 2024)	Retaliation leads to wildlife injury and mortality (Mariki et al. 2015)	Elephants more likely to raid crops during drought (Mariki et al. 2015)	Lack of natural resources for wildlife is a public health concern
Ecotourism	Livelihood benefits (Das and Chatterjee 2015)	Stress and anxiety from feeding by tourists (Maréchal et al. 2011)	Tourist trampling of vegetation	Distanced wildlife viewing might minimize health risks while preserving local economic benefits
Food provisioning	Pleasure and relaxation (Cox and Gaston 2018)	Promotes opportunities for pathogen transmission (Murray et al. 2016)	Affects community dynamics (Galbraith et al. 2017)	Restrict and enforce feeding regulations, communicate less risky contexts (not during pathogen outbreak, in times of resource need, species-specific)
Wildlife gardening (i.e., habitat stewardship)	Feelings of pride and gratification (Goddard et al. 2013)	Species-appropriate food resources (Seress et al. 2018)	Supports biodiversity (Mumaw and Mata 2022)	Lower barriers to wildlife-friendly gardening through free workshops and public spaces (e.g., community gardens)
Household pests	Zoonotic pathogen transmission from commensal rodents (Himsworth et al. 2013)	Predators exposed to anticoagulant rodenticides exhibit immune dysfunction (Serieys et al. 2018)	Anticoagulant rodenticides detected in 94 species across trophic levels (Nakayama et al. 2019)	Invest in nonpesticide methods, emphasize exclusion and attractant removal
Hunting	Food safety concerns for hunters and zoonotic pathogens (e.g., chronic wasting disease; Uehlinger et al. 2016)	Hunting used as a tool to manage disease spread (Miguel et al. 2020)	Scavengers ingesting lead from lead-based hunting ammunition (Hampton et al. 2022)	Phase out lead ammunition, avoid moving animals to new areas for hunting, communicate safe handling practices
Livestock depredation	Economic loss and food insecurity (e.g., hyena and lion predation in Botswana, Kgathi et al. 2012)	Carnivores in poor condition more likely to kill livestock (Luque-Machaca et al. 2023)	Prey abundance reduces carnivore reliance on livestock (Janeiro-Otero et al. 2020)	Preventing wildlife health threats may reduce carnivore reliance on livestock
Physical attacks on humans	Injuries and death (Conover 2019)	Neurological diseases reduce wariness toward people (Sinnott et al. 2022)	Killing elephants motivated in part by retaliation (Mariki et al. 2015)	Preventing neurological diseases in carnivores may reduce attacks
Waste scavenging	Scavengers remove carcasses as source of pathogens (Sonawane et al. 2021)	Unhealthy animals more likely to seek out human-associated foods (Murray et al. 2015a)	Scavengers promote nutrient cycling and food web stability (Beasley et al. 2019)	Reduce wildlife access to human-associated foods to prevent food conditioning
Wildlife–vehicle collisions	Human injury and mortality from collisions (Conover 2019)	Deer severely diseased with Chronic Wasting disease are more likely to be involved in vehicle collisions (Krumm et al. 2005)	Barrier to animal movement (Jacobson et al. 2016)	Preventing the spread of neurological diseases (e.g., moving or feeding deer) may reduce some collisions
Wildlife viewing	Mental restoration, emotional connection (McIntosh and Wright 2017)	Disturbance from recreation (Taylor and Knight 2003)	Wildlife recreationalists over four times more likely to exhibit proenvironmental behaviors (Cooper et al. 2015)	Remove barriers to wildlife viewing for low-income or racialized communities, encourage low-disturbance viewing practices
Wildlife trade	Risk of zoonotic spillover (Shivaprakash et al. 2021)	Pathogen transmission among species (Waldman et al. 2001)	Pathogen pollution (Waldman et al. 2001)	Restrict and enforce trade regulations

use (Steinberg et al. 2015). Messaging about health risks and benefits should be evidence-based and actionable to avoid fear mongering and feelings of helplessness. For example, in Mumbai, India, a series of workshops for media staff led to coverage of jaguar attacks that was less sensational and featured how human actions can contribute to attacks (Hathaway et al. 2017). Actionable recommendations can help demonstrate how human actions affect wildlife health, intentionally or otherwise.

Implications for environmental justice and health equity

Our framework highlights several lines of enquiry to address ongoing environmental justice issues leading to health inequities on the basis of HWIs (figure 2). In terms of the influence of HWIs on human health, it is critical to consider who disproportionately experiences the health benefits and risks of living with wildlife? People are at higher zoonotic disease risk following HWIs that result in direct contact with wildlife, biological material such as feces or meat, and pathogen vectors. As such, contexts with high concentrations of people, wildlife, and their waste—such as cities or the agriculture-wildland interface—convey higher risk (Plowright et al. 2021). Within cities, income disparities also affect exposure to disease vectors because people who are unhoused are disproportionately more likely to come in contact with rats, fleas, and mosquitos (Waddell et al. 2024). Cities are disproportionately more likely to be inhabited by zoonotic disease hosts (Gibb et al. 2020); however, urban wildlife are also more likely to be studied for zoonotic pathogens, biasing research effort (Albery et al. 2022). In US cities, urban neighborhoods that are whiter, more affluent, or gentrified (Fidino et al. 2024) can have more diverse communities of plants (Hope et al. 2003), birds (Loss et al. 2009), and mammals (Magle et al. 2021). This phenomenon is broadly known as the *luxury effect* (Leong et al. 2018), although recent scholarship emphasizes power rather than socioeconomic (Poulton Kamakura et al. 2024). Given that exposure to biodiversity such as birds can promote mental and physical health benefits (Methorst 2024), these inequities in nature experiences may have knock-on effects for public health.

Outside of cities in agricultural and other resource-based landscapes, human communities also differ in their likelihood of coming into close contact with wildlife on the basis of livelihoods and biome. For example, farmers in tropical forest regions are more likely to work near biodiversity hotspots where risk of pathogen spillover is higher (Allen et al. 2017) and farmers in low-income economies are between two and eight times more likely to experience cattle depredation leading to food insecurity relative to farmers in high-income economies (Brackowski et al. 2023). Farmers in areas with large mammals, such as elephants raiding crops in rural Ghana, can face human health risks along multiple pathways. Not only can fearing potential crop loss lead to increased stress and anxiety, but when crops are destroyed, food insecurity rises, contributing to human malnutrition (Galley and Anthony 2024). Moreover, reducing the likelihood of crop raids via nighttime surveillance of fields can result in increased risk of malaria and sleep deprivation, leading to unhealthy coping mechanisms such as alcohol abuse, which, in turn, affects human physical, mental, and economic well-being (Galley and Anthony 2024). Therefore, the contexts conveying increased health risks associated with HWIs are diverse—ranging from unhoused individuals and rat fleas (Waddell et al. 2024) to farmers guarding against elephants—and highlight the nuance needed in predicting the

relative benefits and costs of living with wildlife in different ecological and social contexts.

When thinking about the benefits and risks of living with wildlife, we must also understand who lives in areas with degraded environmental health and why? Communities and individuals face unequal outcomes of HWIs because of socioeconomic inequities and other heterogeneous vulnerabilities, so mitigating harms and fostering benefits in these contexts may be key for increasing equity (Harris et al. 2023). Humans and wildlife are differentially exposed to noise and light pollution arising from inequality between neighborhoods on the basis of socioeconomic as well as historic and ongoing racial discrimination (Cushing et al. 2015, Schell et al. 2020). In the United States, historically redlined neighborhoods (i.e., neighborhoods considered high risk for homeowner loans, often on the basis of racist criteria, Fishback et al. 2024) have higher levels of noise pollution, greater environmental pollution, higher temperatures, and less vegetation (Collins and Grineski 2024, Estien et al. 2024). Light and noise pollution suppresses immune functioning in rodents (Bedrosian et al. 2011), birds (Brumm et al. 2021), fish (Masud et al. 2020), and people (Abouee-Mehrizi et al. 2022, Walker et al. 2022), while also altering circadian rhythms, disrupting endocrine function, and elevating cancer risk (Sanders et al. 2021), all of which alter disease dynamics for humans and wildlife. Unequal exposure to environmental disamenities underscores the need to center the principles of environmental justice within One Health work (Murray et al. 2022).

Unequal access to resources can also affect health equity after HWIs have occurred. Considering human responses to HWIs, which individuals and communities can respond to HWIs in ways that protect human and wildlife health? For example, people that have been excluded from nature experiences on the basis of race or income may have little exposure to educational materials about zoonotic risks from wildlife (e.g., ticks and Lyme disease, Halsey et al. 2023). Socioeconomics also may limit a person's ability to exclude undesired wildlife from their home on the basis of affordability or renter status. Similarly, sociodemographics can influence a person's ability (i.e., social capital) to engage with wildlife management such as reporting negatively perceived HWIs. For example, individuals may not feel comfortable engaging with wildlife managers if they are undocumented immigrants or have had negative experiences with law enforcement based on racial discrimination. Proactive campaigns to ensure everyone can engage with wildlife management would improve wildlife coexistence and public health.

Thinking more broadly about equity in One Health, it is also important to understand which human communities have the capacity to connect with nature in ways that promote healthy people, animals, and environments? Many communities are excluded from nature experiences on the basis of their location or abilities because of discriminatory practices in the location or accessibility of green spaces (Klompmaaker et al. 2023, Winkler et al. 2024). Fostering human-nature connections is an important step in promoting habitat stewardship and human-wildlife coexistence. However, these human-nature connections must be supported by evidence-based approaches that minimize health risks and ensure equitable access to nature. To realize these possibilities, research and management initiatives should include community leaders that can articulate local concerns pertaining to HWIs and barriers to nature (e.g., perceived safety in green spaces, perceptions of wildlife) for marginalized groups. Such partnerships should actively engage with teachings of Indigenous scholars to benefit from the long history of Indigenous knowledge about

the interconnectedness of human and nonhuman life (Landry et al. 2019).

Implications for coexistence

Our framework informs research and practice aimed at human-wildlife coexistence, the goal of which is to manage shared landscapes in ways that foster the health and well-being of both people and wildlife (Carter and Linnell 2016, Frank et al. 2019). Human tolerance for wildlife is key to coexistence, particularly in human-dominated landscapes (Kansky et al. 2016, Puri et al. 2024). Favorable emotional responses to wildlife promote greater tolerance and support for conservation (Larson et al. 2016, Castillo-Huitrón et al. 2020), as well as efforts to address health concerns through nonlethal means. For example, perceived safety risks from wolves is a stronger determinant of support for nonlethal management, relative to social factors such as whether they hunted or kept livestock (Bruskotter et al. 2009). Public tolerance for wildlife is often more strongly associated with intangible risks to health and safety and nonmonetary benefits such as positive emotions rather than monetary damages or incentives (Kansky et al. 2016, Kansky et al. 2021). Therefore, understanding the health risks and benefits people perceive and experience with respect to HWIs is critical to building tolerance and public support for coexistence.

Although the wildlife management literature has been focused mainly on HWIs that are perceived as negative, the forms and outcomes of HWIs are diverse (Soga and Gaston 2020). The broader framing of managing HWIs for coexistence has increased attention to positive interactions and outcomes (Frank et al. 2019, Pooley et al. 2021). This shift in emphasis has coincided with increased attention to the positive health impacts of nature experiences, which Bratman and colleagues (2019) referred to as *psychological ecosystem services* because of the mounting evidence of the positive physiological, affective, and cognitive benefits of interacting with nature. With the aim of human-wildlife coexistence, our framework highlights not only negative interactions and outcomes but also the potential for positive interactions and outcomes. This diversity in outcomes is also reflected in the complex and diverse human responses to HWIs. These responses, which could range from culls to habitat stewardship, can reflect a balance between managing health risks and benefits for humans (e.g., zoonotic diseases, attacks), wildlife (e.g., pathogen transmission), and the environment (e.g., species overabundance). With a comprehensive view of health, potential benefits to human well-being include physical, mental, social, and spiritual elements that could motivate landscape and wildlife management for the benefits of people and wildlife, rather than narrowly focusing on negative interactions or conflicts that arise from physical interactions between wildlife and people. Although the latter have been a primary focus of human-wildlife research and management, we posit that a more holistic approach inclusive of all interactions and outcomes could help shift the public discourse and management strategies away from conflict and zoonosis toward win-win interactions and outcomes that improve the well-being of both people and wildlife.

With a coexistence approach, we recognize that HWIs involve some level of conflict and risks that are dynamic over time but require ongoing proactive engagement. Interdisciplinary teams can help facilitate such proactive actions. For example, a participatory community action project in Uganda implemented proactive mitigation strategies (trenches, beehive fencing, buffer crops, cash crops) to reduce the human health impacts of crop raiding by elephants (McCarten and Milich 2023). The participants reported improved diet, sleep, stress, exposure to zoonotic diseases, and in-

come stability, demonstrating how proactive strategies to reduce HWIs can benefit diverse aspects of human health and coexistence. Proactive management with support from interdisciplinary teams can help move communities beyond fear and reactive management interventions to a cycle wherein positive interactions between people and wildlife can benefit public health and foster positive attitudes toward conservation (Buijs and Jacobs 2021).

Future directions to promote health equity and human-wildlife coexistence

Future research can help address gaps in our understanding of how HWIs affects—and is affected by—human, animal, and environmental health. For example, more work is needed to understand the causal mechanisms underlying the association between wildlife health and HWIs. This focus would identify in what contexts animals are more likely to become unhealthy because of HWIs (e.g., pathogen transmission from food provisioning), in what contexts unhealthy animals are more likely to be involved in HWIs (e.g., seeking out human-associated foods), and if unhealthy animals are more likely to be involved in HWIs because of behavioral changes associated with poor health or if they are unhealthy because of prior HWIs. Longitudinal data on individual animals are needed to address these questions. For example, the mountain lion P22 in Los Angeles was more likely to use urban areas during periods when he was in poor health, which was revealed through 10 years of tracking data (box 2). Although time and labor intensive, behavioral data on individual animals over ecologically relevant timescales can help identify causes of behavioral shifts that may lead to negatively perceived HWIs.

Future studies also might address the role of health in decision-making about wildlife management. For example, how are resources allocated among management actions that prevent wildlife health risks relative to lethal management of infected or potentially exposed animals? Similarly, how do outward signs of disease inform the acceptability of lethal wildlife management and does this differ for zoonotic and nonzoonotic pathogens? In the context of recreation and ecotourism, how can we develop and enforce regulations to maintain human health benefits from HWIs while minimizing the likelihood of health risks for people and wildlife? Such lines of enquiry can help guide proactive wildlife management that protects human and wildlife health.

Finally, a pressing area for future research is advancing health equity at the intersection of health and HWIs. Addressing the sources of inequality that prevent access to the health benefits of HWIs, that increase the risks of HWIs, and that reduce one's capacity to engage with management are important to foster health equity and require partnerships with community leaders, urban planners, and public health agencies. Thinking globally, it is critical to identify communities that are particularly vulnerable to health harms from HWIs arising from urban sprawl into biodiversity hotspots, extreme weather from climate change, and lack of financial or institutional support for mitigating HWIs. Conversely, it is also important to learn from the contexts in which HWIs bring joy, relaxation, restoration, and reduced zoonotic risk so that they might be encouraged elsewhere.

Our framework highlights the integrated connections between health and HWIs to help understand the role of health as both an outcome and driver of HWIs in a world facing dramatic changes in land use, climate, and worsening health equity. Acknowledging the connections and feedback loops among HWIs and human health risks or benefits, human actions in response to those risks or benefits, wildlife health and behavior, and environmental

health will help promote beneficial health outcomes and anticipate health harms for people and wildlife. A more holistic and equitable approach to One Health and HWIs will improve wildlife conservation, public health, and human–wildlife coexistence in diverse contexts around the world.

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