REVIEW



Opportunities and challenges with growing wildlife populations and zoonotic diseases in Sweden

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Abstract In many parts of Europe and North America, populations of large mammals and birds have recovered during recent decades. In Sweden, this has resulted in more wildlife than was historically recorded. This positive development provides a number of opportunities for ecosystem services and for biodiversity. More wildlife also means more interactions with humans, as many birds and mammals may interfere with human interests in the landscape, such as natural resource use. Thus, more wildlife may shift the baseline for societal perception of wildlife. Wildlife species may host pathogens with potential for infecting humans and domestic animals. With increasing knowledge about zoonotic diseases and their dynamics, more scientific, media, and public attention is given to zoonotic processes. We are concerned with how the public image of the wild animals is affected, because many of the recent zoonotic outbreaks connect animal groups to diseases such as avian and swine influenza, lyme disease, and tickborne encephalitis. The societal focus on zoonotic diseases may increase the fear of the wild and will separate the public further from the outdoors in general and wildlife in particular. Ultimately, we risk a juxtaposition of the overall acceptance of biological diversity and a shifting societal perception of wildlife that could be harmful for life on earth. We therefore suggest multidisciplinary research on societal awareness of

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Carl-Gustaf Thulin carl-gustaf.thulin@slu.se zoonotic diseases and its implications for public acceptance for wildlife and biological diversity.

Keywords Attitudes \cdot Biodiversity \cdot Ecosystem services \cdot Public \cdot Wildlife \cdot Zoonoses

Introduction

The global ecosystem is dominated by human activities that directly or indirectly affect the conditions of other organisms (Vitousek et al. 1997). Thus, every section of the global ecosystem has its own history and trajectory, permeated by the human influence imposed since humans colonized the globe. Our responsibility as a species with major influence on global development is to implement sustainable prerequisites for life on earth, ourselves included. The Brundtland report from 1987 proposed that environmental sustainability is the key to a durable future for humans as well as other organisms (Brundtland et al. 1987). Sustainability is an accepted but highly debated concept with no consensus over the societal goals (Connelly 2007). Attitudes may be considered reflections of societal sustainability, i.e., if something is generally accepted its eventual implementation is more likely and vice versa (Heberlein 2012).

Human expansion throughout the world is believed to have triggered extinction of several large mammal species (Martin 2005). In many regions, this extinction is still progressing at an alarming pace (Dirzo et al. 2014; Ripple et al. 2015), but there are also examples of recovering wildlife, in particular in Europe and North America (Apollonio et al. 2010; Deinet et al. 2013; Brown 2013; Chapron et al. 2014). Several large birds and mammals are valuable for human well-being because they provide ecosystem services, typically divided in provisioning, regulating, cultural, and supporting

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(Millennium Ecosystem Assessment, 2005). Large birds and mammals do, however, also challenge our own interests in the ecosystem and our use of natural resources. Thus, they challenge our attitudes towards what is an acceptable wildlife impact on humans and society. To widen our understanding of the intrinsic thresholds of this acceptance, we review the potential benefits and challenges posed by recovering wildlife populations, with emphasis on their development in Sweden and how the public attitude towards wildlife may be affected by reports on zoonotic diseases.

The recovery of Swedish wildlife

From the end of the eighteenth century, many large mammals in Sweden suffered from uncontrolled hunting and fatal interference with human interests. In the wake of the French revolution, the Swedish king Gustav III decided in 1789 that hunting rights, heretofore exclusively granted to major landowners like the royal and noble families, were given to all landowners (Danell et al. 2010). Consequently, in a few decades, populations of moose (Alces alces), red deer (Cervus elaphus), and roe deer (Capreolus capreolus) were driven towards extinction. The native wild boar (Sus scrofa) was already extinct in Sweden by the seventeenth century, and the last wild beaver (Castor fiber) were shot during the nineteenth century. Roe deer and red deer were finally protected in the middle of the nineteenth century, at population sizes below 100 individuals (Ahlén 1965; Liberg et al. 1994). The pattern of survival of the moose is unclear, but likely a few remnant moose populations/specimens were spared in remote areas.

As a consequence of the disappearing large wild herbivores, large mammalian predators became an increasing obstacle to husbandry (cf. Kardell and Dahlström 2013). Bounties were generous and hunts (drives), organized by the forest administration, were mandatory (Kardell and Dahlström 2013). Bounties for gray wolf (*Canis lupus*) remained until December 31, 1965, when the wolf received legal protection from January 1, 1966 (Wabakken et al. 2001). The wolf is believed to have been functionally extinct in Sweden until 1984 (Wabakken et al. 2001). All large mammalian predators: wolves, brown bears (*Ursus arctos*), lynx (*Lynx lynx*), and wolverines (*Gulo gulo*), reached minimum population levels during the mid-twentieth century.

Starting in the early twentieth century, Swedish wildlife has recovered as a result of regulated hunting, protection, and legislation focusing on restoring of habitats (Danell et al. 2010). Browsers, such as moose and roe deer, were aided by selective hunting that focused on juveniles and sub-adults, an acreage-based hunting quota, and by large-scale forest clearcuts (Cederlund and Bergström 1996; Ericsson et al. 2000). The forest clear-cuts provided an overflow of high-quality feed during the 5–15-year regeneration phase, and the mosaic landscape of regeneration forests served as both feed and shelter. In the 1980s, the winter moose population in Sweden reached over 500,000 individuals, i.e., more than 1 moose/km² [total area of Sweden is 449,964 km², of which 8.7 % is water]. Similarly, the roe deer population also benefitted from the absence of large predators and the introduction of sarcoptic mange, which devastated the red fox (*Vulpes vulpes*) population (Lindström et al. 1994). After unusual mild winters during the mid 1990s, the number of roe deer reached more than a million individuals during the winter (Liberg et al. 1994).

The recovery of the red deer was partially aided by supplementary release of individuals imported from outside of Sweden (Höglund et al. 2013). The population of red deer is still increasing, particularly in southern and central Sweden. Wild boar were reintroduced to Sweden in 1976 (Welander 2000), and game bag data from the Swedish Association for Hunting and Wildlife Management show that currently around 100,000 wild boar are harvested annually (http://jagareforbundet.se/ vilt/viltovervakning/historisk-avskjutning/). Beaver were reintroduced in 1922 and occur today over most of the country (Hartman 2011). Fallow deer (Dama dama), a nonnative species first introduced during the seventeenth and eighteenth centuries, are increasing in numbers as well (cf. Kjellander et al. 2012), and during the last 20 years, populations of mouflon (Ovis orientalis) occur locally, mostly as a result of accidental escapes from enclosures. In addition, most populations of wild geese have reached higher numbers, primarily following protection and shifted agricultural practices (Nilsson 2013).

In the wake of herbivore population recovery, all large mammalian predators have also increased in numbers. Wolves returned by recolonization from the east (Finland and Russia), and the current population counts approximately 400 individuals (Svensson et al. 2013). In addition, bear, lynx, and wolverine populations have increased in Sweden (Kaczensky et al. 2012). The red fox population has recovered from the sarcoptic mange outbreak in the 1980s, the European otter (Lutra lutra) population is now sustainable following protection, a recovery program, and a less polluted environment, golden- and white-tailed eagles (Aquila chrysaetos and Haliaeetus albicilla, respectively) have increased following protection, prohibition of toxic chemicals, and supplementary feeding, and the three seal species-harbor seal (Phoca vitulina), ringed seal (P. hispida), and grey seal (Halichoerus grypus)—occurring along the Swedish coasts have recovered from overharvest and pollutants (primarily DDT and PCB).

In brief, Sweden is currently likely to host the greatest number of large, wild birds and mammals seen during the last 500 years, perhaps even thousands of years. The positive Swedish trends observed in wildlife numbers and expanding populations are similar to what is documented in other parts of Europe and North America (Apollonio et al. 2010; Kaczensky et al. 2012; Deinet et al. 2013; Brown 2013; Chapron et al. 2014). However, the combination of large wildlife populations, a relatively strong economy, and a cultural history of being close to nature, hunting, wildlife viewing, and other outdoor activities make Sweden a conceptually interesting model for the shift in wildlife numbers and examinations thereof.

Ecosystem services of wildlife

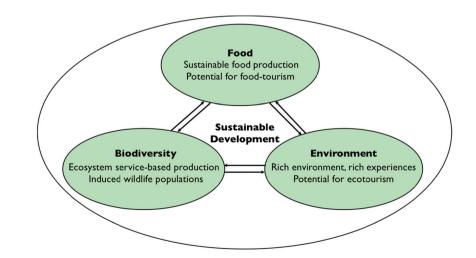
The increase of Swedish wildlife populations offers several ecosystem services. Wildlife in Sweden generate close to 20 million kg of meat annually (Lööv et al. 2013), and 65 % of Swedes 16-65 years of age eat meat from wildlife at least once annually (Ljung et al. 2012). Moose provide most of the game meat, with approximately 10 million kg (bone-in carcass weight), followed by wild boar at about three million kg, and then by other ungulates, in particular roe deer, red deer, and fallow deer. The growing populations of geese offer a largely unexploited opportunity to harvest fowl meat, while other waterfowl (mallards, teals) and Galliformes (capercaillie, grouse, ptarmigan) provide exclusive niche dishes. In general, game meat attracts attention in a growing restaurant and food tourism trend, focusing on exclusive dishes based on regionally produced food. Although not extensively exploited in modern society, skin (hides) and furs are other products from both herbivores and predators, given a sustainable management and resource utilization.

In addition to meat and skin, wildlife provide a variety of opportunities for a growing ecotourism industry (Lovelock 2015). A national survey in the USA in 2011 revealed that over 90 million residents above age 16 enjoyed some form of wildlife-related recreation, with an economic turnover of amounting to US\$145 billion ("2011 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation" Anonymous (2011). Wildlife watching was most popular, followed by sport fishing and hunting. In Europe, wildlife tourism, in particular wildlife watching, is still underdeveloped but holds a large potential (sensu Sylvén and Widstrand 2013; Lovelock 2015). In Sweden, moose has become a flagship species for tourists, with images of moose on a diversity of products and advertisements and with moose pellets and road signs that alert for moose crossings sold as souvenirs. The current ecotourism in Sweden is primarily directed to attract Nordic, European, and North American visitors, but increasingly also tourists from Asia, particularly China. The Rewilding Europe initiative primarily aims to explore the ecotourism opportunities proved by wildlife (Sylvén et al. 2010), and in many ways the pattern of wildlife recovery in Sweden could serve as a model for this development.

As opposed to hunting, wildlife watching is less invasive, since it mainly aims at observing or listening, sometimes during hiking, but often from vehicles (which leads to challenges with respect to emissions, e.g., Lovelock 2015). Because of the impact of hunting on, for example, animal behavior, areas of strict protection of wildlife have been proposed (e.g., Deinet et al. 2013). Nevertheless, there are opportunities in the combination of observation and harvest depending on how wildlife management is oriented. In Sweden, most of the licensed and temporally regulated hunting is conducted during the autumn and winter (Mattsson et al. 2008), thus enabling a combination with wildlife observation in spring and summer (the primary tourist season), creating a triangular opportunity for biodiversity, multipurpose land use (e.g., food production), and ecotourism combined (Fig. 1). Or, to put this in monetary terms, a wild boar can be sold as an ecotourism experience in the spring, for hunting in the autumn, and as food in the winter; meanwhile, wild boar plow, sow, and fertilize the land.

Wildlife watching is often focused on or primarily directed towards large predators. Because of the nature of predatorprey relationship, the top predators may serve only as a zest for any ecotourism adventure, and numbers of herbivorous prey are fundamental as guarantees of a wildlife experience (i.e., predators are rare and enigmatic, and thus rarely seen;

Fig. 1 Wildlife provides a triangular opportunity for uncultivated food production, prerequisites for biodiversity and rich environment with opportunities for different sorts of ecotourism (e.g., wildlife watching, hunting, wild food), all in all a sustainable form of multipurpose, areal land use



ungulates are common and more easily observed). An ecotourist may be satisfied by the notion of wolves being "out there," somewhere, perhaps seeing some tracks, but can be guaranteed to bring home the experience of seeing beavers in a watershed or moose browsing a meadow in the forest.

From a holistic perspective, the regulating and supporting ecosystem services provided by large mammals and birds are perhaps more interesting and intriguing. Keystone herbivores and predators may regulate structure and function of ecosystems and, thus, enable long-term persistence of a variety of other, less apparent animal species, vertebrates, and invertebrates, as well as plants and fungi, all in all creating a basis for preservation of biological diversity in general (e.g., Estes et al. 2011; Ripple et al. 2014; Sandom et al. 2014). Large ungulates, grazers, and browsers, may aid in the preservation of steadily reforested open landscapes (i.e., meadows and pastures deserted by domestic husbandry), spreading seeds of various herbs and grasses, creating mosaics by browsing, grazing, rooting, and trampling, and fertilizing by spreading excrement (Welander 1995; Rook and Tallowin 2003; Speed et al. 2010; Speed et al. 2014). Similarly, large concentrations of waterbirds provide several regulating and supporting ecosystem services (e.g., Green and Elmberg 2013).

Finally and perhaps most importantly from a societal perspective, a feature of Swedish wildlife is the widespread distribution and proximity to public life, i.e., most wildlife species, herbivores, and predators alike are not confined to specific national parks or wildlife refugee areas but rather may be observed close to all major cities, on public, as well as private land. Because of this physical proximity, the public's opportunities to observe wildlife and interact with wilderness is likely an important cultural ecosystem service that forms a platform for general acceptance of biological diversity as a whole (Heberlein and Ericsson 2005; Ljung et al. 2015). In combination with other cultural ecosystem services such as hunting, fishing, and even religious belief based on experience and proximity to nature, the cultural perspectives are perhaps the most societally penetrating consequences of a rich variety of wildlife.

Management challenges with growing wildlife populations

Increasing wildlife populations provide a number of management challenges (Apollonio et al. 2010), such as management of wildlife damage, that generate conflict between humans and wildlife and require a program of management entailing sustainable harvest or population control. The latter involves a mental shift from protection and conservation to harvest and regulation. This phenomenon has been described as the "last settler syndrome" (Nielsen et al. 1977). Nielsen et al. (1977) developed a scenario first described by White (1971); "Each wants his particular town and country landscape to remain just as it was when he or she arrived. The most recent settler wants to be the last settler." The observation by White (1971) stems from the development of a watershed management plan, but it may be transferred to any kind of first perception, e.g., a perception of the status of wilderness or "crowdedness" that the first settlers in an area experience (Nielsen et al. 1977). This first impression, often combined with a love of the land such as it first appears, tends to imprint the human mind, so that any shift of status, e.g., recombination of people, landscape features, or wildlife, tends to obscure the beauty. Pauly (1995) take this concept closer to practical management by describing a shifting baseline syndrome with relation to fisheries practices, i.e., preferences of fishermen for particular target species shift over generations (of humans) to cope with changes in resource numbers and species composition.

The shifting baseline syndrome of fisheries developed by Pauly (1995) has many analogies with management challenges involved with increasing wildlife populations (Morrison 2009; Jachowski et al. 2015). However, apart from ways to use the resource, there are also challenges involved with other forms of areal land-use developed in the absence of numerous wildlife species (Martinuzzi et al. 2015). In the absence of large carnivores, hunting practices and animal husbandry have developed in such a way that the current situation creates obstacles (Ericsson and Heberlein 2003a; Dressel et al. 2015). In particular, semi-feral, domestic husbandry, such as reindeer herding and traditional, feral pasture grazing (in Swedish *fäbodbruk*) is difficult to combine with vibrant populations of large predators (Dondina et al. 2015). Similarly, conventional land use such as modern forestry and agriculture is challenged by wild herbivores, sharing the resources and taking advantage of anthropogenic practices in a landscape that is often deprived of biological diversity and, thus, alternate resources (e.g., Edenius et al. 2014). Also, large mammals provide obvious risks for the car-bound human population and airplane collisions with geese, swans, and cranes are also dangerous (e.g., Neumann et al. 2013).

Disease transfer between wildlife and domestic livestock is another important issue in the management of wildlife. Gortázar et al. (2007) define five areas of primary concern: (1) introduction of diseases through movements or translocations, (2) consequences of wildlife overabundance, (3) risks with free ranging livestock production, (4) vector expansion, and (5) host expansion or introduction. The challenges are bidirectional, i.e., risks for livestock to be infected by wildlife vectors and subsequently also humans (see below), and risks for wildlife populations to be infected by domestic vectors (e.g., Rossi et al. 2007; Treanor 2013; Lescureux and Linnell 2014). Disease transmission from wildlife to livestock may also counteract conservation efforts because of lowered public acceptance (Brook and McLachlan 2006). Finally, the risk of transferring disease from wildlife to humans, e.g., zoonoses, is perhaps one of the most severe challenges with rich wildlife populations (e.g., Jones et al. 2008; Langwig et al. 2015).

Zoonoses and the public

As much as 60 % of emerging infectious diseases between 1940 and 2004 are believed to have a zoonotic origin (Jones et al. 2008). The majority of those, 72 %, stem from humanwildlife interactions (Jones et al. 2008), with an increasing trend during the latter decades (Wilcox and Gubler 2005). Zoonotic diseases have also been transferred from domesticated animals during the development of agriculture and husbandry. Taylor et al. (2001) showed that 868 out of 1415 (61 %) species of infectious organisms known to be pathogenic to man have a zoonotic origin, and King (2004) predicts an increasing trend. The World Health Organization recognizes emerging zoonotic diseases as a global concern for human health, with potential for significant economic impact (www. who.int).

As our knowledge about zoonotic diseases and their dynamics develops, there is increased scientific, media, and public attention given to zoonotic processes. In tackling a challenging zoonotic outbreak, an established discover-to-control routine is a crucial path to controlling the emerging situation (Tabbaa 2010). Thus, at first sign of disease, investigations that focus on the infectious pathways are needed (Glik 2007). A second effort is communication to the public through media (Hyer and Covello 2005).

The public awareness and attention to zoonotic wildlife diseases and outbreaks are justified from a public health perspective (Decker et al. 2011; Langwig et al. 2015). With a steadily increasing global human population, the risks and impacts of zoonotic diseases accumulate (Wilcox and Gubler 2005). An additional factor is the increasing consumption of meat, which in particular, when poor food safety prevails, induces our exposure to animal proteins and, thus, enables potential for transmission through our digestive system (e.g., Genigeorgis 1987; Schlundt et al. 2004). However, the instant communication of an emerging zoonotic outbreak provides some perplexing aspects with respect to public attitudes. As many of the recent zoonotic outbreaks lead to an association of particular animal groups with a given disease, e.g., avian and swine influenza, lyme disease, and tick-borne encephalitis, it is relevant to be concerned with how our image of the wild animals and the wilderness they inhabit is affected. Moreover, a comparative ecosystem approach to the dynamics of zoonotic diseases in industrial food-animal production systems indicates that the role of wildlife is overemphasized (Leibler et al. 2009). Thus, wildlife seems to be accused disproportionately because of a tendency to blame the unknown (Fig. 3).

Public and the wild

In Sweden, there is a legal right of common access to public and private land, "Legal Right of Access to Private Land" [from Swedish *Allemansrätten*], which enables people to explore nature areas freely and also to pick wild berries and mushrooms (Sandell and Fredman 2010). This legal right has most likely contributed to a relatively strong societal interest and passion for nature and wildlife.

The public shows tendencies of transposition from utilitarian to mutualistic following increased economic welfare (Teel and Manfredo 2010). The "utilitarians" learn about wildlife from direct experience, while "mutualists" tend to base their learning on social interaction. An anthropographic map of Sweden shows a difference between urban and rural areas in that rural residents spend on average more time in the outdoors than urban citizens (Ericsson and Heberlein 2003b; Heberlein

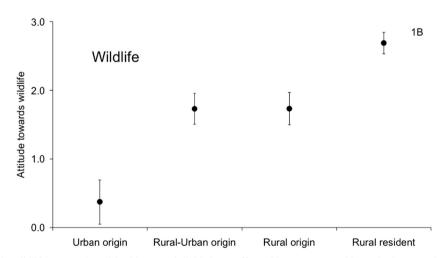


Fig. 2 Attitudes towards wildlife among Swedish citizens, subdivided into categories "urban origin" (more than three generations), "rural-urban origin" (one to three generations since move to city), "rural origin" (<1 year), and "rural residents". *Y*-axis=0 refers to neutral attitudes towards wildlife, with increasingly positive attitudes. Thus, there is an

effect with respect to positive attitudes towards wildlife of being brought up in urban areas (N>10,000) that goes back at least three generations (i.e., category "rural-urban"), while citizens with urban longer history tends to be neutral. Adopted from Heberlein and Ericsson (2005)

and Ericsson 2005; Ljung et al. 2015). The mean national interest in outdoor activities, measured as "spending time outdoors at least once/year," is estimated at 85 %, while citizens in remote rural areas approach 96 % and in, e.g., central Stockholm (capital of Sweden), only 72 %.

Similar trends are to be found in the attitudes towards wildlife among Swedish citizens. When citizens are subdivided into categories "urban origin" (more than three generations), "rural-urban origin" (one to three generations since move to city), "rural origin" (<1 year since move to city), and "rural residents," there is a decrease in positive attitudes; the longer time is spent away from rural areas (Fig. 2; adopted from Heberlein and Ericsson 2005). Interestingly, the positive attitudes towards wildlife go back at least three generations (i.e., category "rural-urban"; n > 10,000), while citizens whose families have been urban citizens longer than three generations tends to be neutral (Heberlein and Ericsson 2005).

In Sweden, there is a tendency for people to "fear the unknown," i.e., any species with a recent expansion in numbers (e.g., wolf, wild boar) tends to intimidate people more than a species that has been present and well known for longer, such as moose (Ericsson et al. 2010). Moose recovery in Sweden mainly happened prior to 1980s, when the national surveys of attitudes started (Norling et al. 1982), and moose have since decreased in numbers on a national scale (Hörnberg 2001). Thus, attitudes towards recovered historical moose populations are not covered by any national surveys.

Direct disease transmission between wildlife, livestock, and humans and the reciprocal perceptions that underlie human attitudes towards wildlife likely differ in magnitude (Fig. 3). Thus, while the zoonotic impact of wildlife is important to consider, it is given relatively larger attention than industrial animal husbandry (e.g., Leibler et al. 2009) from the public and thereby induce shifts in attitudes. People who lack knowledge and experience are more inclined to blame the unknown, in our case, wildlife.

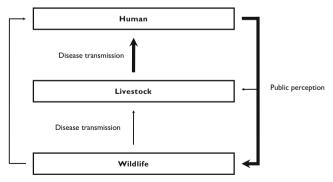


Fig. 3 Schematic overview of direct disease transmission between wildlife, livestock, and humans and reciprocal perceptions that underlie human attitudes towards wildlife. Thus, the zoonotic wildlife impact is important to consider but is given relatively larger attention from the public that risk to induce shifts in attitudes. The *arrows* are hypothetical, not reflecting actual proportions

Conclusions

Growing populations of wildlife provide new perspectives for mutualists (urban) and utilitarians (rural) in Sweden and, thus, shift the baseline for societal perception of wildlife as suggested by Heberlein and Ericsson (2005). As younger generations become less involved in outdoor activities, they disconnect from the wild (Louv 2005), shape their opinion more from what is communicated in media and over the internet, and may form a less rigid attitude than those based on direct experience of nature and outdoor activities. Thus, with a deficit of deeper insights and experiences, it is easier to perceive wildlife as problematic and dangerous (i.e., closer to a baseline shift). Furthermore, if communication is problem-focused towards wildlife in general and diseases in particular, there is an obvious risk for baseline shift in our attitudes towards wildlife (sensu Heberlein 2012). Thus, children who grow up perceiving wildlife as problematic face a greater risk of developing a problematic perspective on wildlife as adults.

One potential outcome of this is an increased awareness and fear of wildlife, in particular in close vicinity to urban areas, houses, and farms. Wildlife disease management should involve proactive risk communication that considers human belief, attitudes, and risk perception (Decker et al. 2006), and wildlife professionals have to be considerate towards public perception when they communicate information about emerging infectious diseases among wildlife (Decker et al. 2011). An aspect to consider is that of short-term interest in acquiring research grants for all well-motivated scientific efforts with regard to zoonotic potential. To acquire headline news for preliminary data may be useful for grant approval but is a risky venture with respect to public attitudes. Thus, a trade-off between public health, research funding, and induced detachment between humans and nature emerges.

It is not clear how much an increased media, scientific, and overall societal focus on zoonotic diseases affects this relationship, but we suggest that it may be significant. We also fear that negative attention and reports affect the overall rationale for preserving biological diversity and may shift the fundamental baseline for societal perception of wildlife. Thus, we risk juxtaposing the overall acceptance for preserving biological diversity with a shifting societal perception of wildlife in a way that could harm life on earth. We urge multidisciplinary research on societal awareness of and attitudes about challenges arising from emerging wildlife populations, in particular zoonotic diseases, and their implications for public acceptance of wildlife and biological diversity.

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