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Not just 'super-predators': human behaviour shapes wildlife behavioural responses across avoidance, tolerance and attraction

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Humans are thought to have a disproportionately negative impact on wildlife and are viewed by some as the ultimate 'super predator'. This view implies that wild animals perceive humans primarily as predators. However, a growing body of evidence shows that wildlife can have remarkable tolerance for, or even attraction to, humans. Here, we present wildlife responses to humans along the avoidance–attraction continuum, to highlight that avoidance, tolerance, and attraction are all within the normal range of wildlife behavioural responses to humans. We embed the avoidance–attraction continuum in a mechanistic framework to understand behavioural responses to humans as the result of a species' evolutionary history and accumulated experiences during their lives. We find that historical and current human behaviour towards wildlife – whether it is aversive, neutral or beneficial to animals – plays an important role in shaping selective pressures and learning outcomes in the focal population. By shifting from a restrictive view of wildlife as inherently fearful of humans to a broader understanding of wildlife responses, we are better able to refine public perception of wildlife behaviour, wildlife management and ecological research, and ultimately promote human–wildlife coexistence.

Keywords: animal personality, behavioural plasticity, behavioural tolerance, ecology and evolution, human disturbance, human–wildlife interactions, wildlife management

Introduction

There is a vast body of literature that documents that wild-living animals can perceive humans as predators, reacting fearfully and avoiding human presence (Frid and Dill 2002). Even non-consumptive activities, such as outdoor recreation, can disturb wildlife, i.e. induce physiological and behavioural changes such as stress or flight, often with (negative) consequences for individual fitness, population persistence and species

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interactions (Ripple and Beschta 2004, Coetzee and Chown 2016, Blumstein et al. 2017, Gaynor et al. 2018, Suraci et al. 2019). For example, Gaynor et al. (2018) have documented pervasive shifts towards nocturnality across many taxa as a strategy to avoid human activity. Furthermore, perceived risk from human activity can create a landscape of fear, where wildlife alter their behaviour and distribution, sometimes more strongly than in response to non-human predators (Ciuti et al. 2012, Clinchy et al. 2016, Gaynor et al. 2019, Moleón and Sánchez-Zapata 2023). Given the ongoing encroachment of human activities into wildlife habitats (Soga and Gaston 2020), human disturbance is a serious conservation concern (Carney and Sydeman 1999, Blumstein et al. 2017). At the same time, there is also a wealth of evidence that wildlife – individuals, populations and species – can be remarkably tolerant of, and even be attracted to, humans (Whittaker and Knight 1998, Samia et al. 2015, Čapkun-Huot et al. 2024). Despite the behavioural ecology literature that demonstrates non-fearful or less fearful behavioural responses of wildlife to humans, recent publications focussing on the particular ecological impact of human 'super predators' (Darimont et al. 2015, Clinchy et al. 2016, Crawford et al. 2022, Zanette et al. 2023) may bias the discussion of wildlife behavioural responses to humans, which in turn, reinforces a standard perception of humans as predators and wildlife as inherently fearful of humans. This emphasis tends to marginalize less-fearful responses as deviations from a perceived norm (Reynolds and Braithwaite 2001, Knight 2009).

Wild animals are assumed to perceive humans as 'risky' predominately due to the historical and ongoing exploitation of wildlife by humans through hunting and trapping (Washburn and Lancaster 1968, Frid and Dill 2002). However, the cultural and societal norms underlying hunting and trapping vary geographically and temporally. Around the world, only a subset of species are targets of hunting and trapping, while some species are protected or revered. Humans may also provide resources or care for wildlife, or desire to cause little to no harm through observational and recreational activities (Storch 2013, Manfredo et al. 2017, Uchida et al. 2023). The substantial differences in how wildlife is – and has been – perceived and treated across human societies are shaped by diverse belief systems, value orientations, and the people's broader social, political and economic contexts (Manfredo 2008, Dickman 2010, Baker et al. 2014, Nyhus 2016, Bonsen et al. 2024). We argue that the portrayal of humans as 'super-predators' skews towards the consequences of utilitarian or dominance values of wildlife, while underappreciating other orientations such as mutualism or intrinsic value orientations (Manfredo 2008). Thus, while the profound human impact on wildlife populations and community dynamics is undeniable, the common assumption and portrayal of humans as predators obscures the nuanced roles that humans play within ecosystems (Moll et al. 2021, Palmer et al. 2022), and, consequently, how wildlife interact with humans (Storch 2018, Lasky and Bombaci 2023).

From a behavioural standpoint, wildlife behavioural responses to human presence can vary from avoidance to tolerance to attraction (see Box 1 for working definitions of these terms as used in this essay). We move away from the restrictive concept and common perception that avoidance of humans is the 'norm' and other behaviours are 'aberrant' or 'exceptions'. Instead, we present wildlife behavioural responses to humans along a continuum spanning from avoidance to attraction to emphasise that different responses on this continuum are equally likely. We suggest that cumulative evolutionary and lifetime experiences with humans – whether harmful, neutral or beneficial – are major factors that influence where an individual, or individuals within a population, or even a species, falls on this continuum.

In the following, we first elaborate on how evolutionary experience with humans can shape a species' innate behavioural phenotype over multiple generations by modifying selective pressures on anti-predator behaviour towards humans. Second, we discuss how present ecological experience with humans can modify innate phenotypes during an individual's lifetime though behavioural plasticity and learning, in particular. While we focus on the strong role of human behaviour (specifically, the type of human activities as related to wildlife), we note that animal behaviour is modulated by multiple factors, such as genetics, epigenetics, demographics, animal physiology and cognition, and/or the environment (Tablado and Jenni 2017, Lasky and Bombaci 2023, Čapkun-Huot et al. 2024). While a full review of potential modifiers is beyond the scope of this paper, we provide a short overview of those in the third section. Finally, we emphasize the need to account for wildlife responses to humans along the entire avoidance–attraction continuum, and for the role that context-specific human activity plays in modifying wildlife behaviour in research, conservation actions and wildlife management.

We predict that aversive experiences with humans such as being hunted or otherwise persecuted will shift behavioural response to humans more towards avoidance on the continuum whereas neutral or beneficial experience with humans should shift behavioural responses more towards attraction (Ydenberg and Dill 1986, Lima and Bednekoff 1999, Storch 2013, 2018, Parsons et al. 2022). To support this prediction, we present multiple case studies documenting diverse expressions of behaviour of different wildlife populations, including different populations of the same species, across this spectrum and relate this pattern to past and present experience with humans, while also considering potential modulators and constrains on behaviour (Fig. 1, Table 1).

Evolutionary experience with humans influences wildlife behaviour across avoidance–attraction

Anti-predator behaviours tradeoff fitness costs and benefits (e.g. avoiding predation while acquiring resources) (Ydenberg and Dill 1986). According to the risk–disturbance hypothesis humans are perceived as predators and prey will display anti-predatory behaviour to humans following similar economic principles as seen in encounters with non-human predators (Lima and Bednekoff 1999, Frid and Dill 2002). These premises are based on the tendency of prey to respond to

Box 1. Working definitions of types of behavioural responses to humans, as used in this essay, corresponding to distinct points along the avoidance–attraction continuum: the outer edges represent strong attraction and avoidance, while the centre reflects tolerance (i.e. an absence of, or low-level, behavioural response).

Term	Definition
Avoidance	Responding to human presence with anti-predatory behaviour such as vigilance or flight, and/or actively avoiding areas with human activity.
Tolerance	Responding to human presence with no, or little, discernible change in behaviour.
Attraction	Responding to human presence by actively seeking out humans and human-dominated areas.

generalised threatening stimuli, such as sudden movement or abrupt sounds, and are grounded in systems where humans have historically hunted or persecuted the species (Frid and Dill 2002). When the expression of heritable anti-predator behaviours are not too costly, or have pleiotropic effects on other traits, they can be maintained even in absence of a current predation risk (i.e. ghost of predators past' Hypothesis, GPP) (Byers 1997, Peckarsky and Penton 1988). Conversely, costly or predator-specific, heritable anti-predator behaviours may be reduced or eliminated by natural selection, when predation pressure is relaxed or absent (Darwin 1859, Magurran et al. 1995, Lahti et al. 2009). There are many examples of this in non-human predator–prey systems (Berger et al. 2001, Beauchamp 2004, Fullard et al.

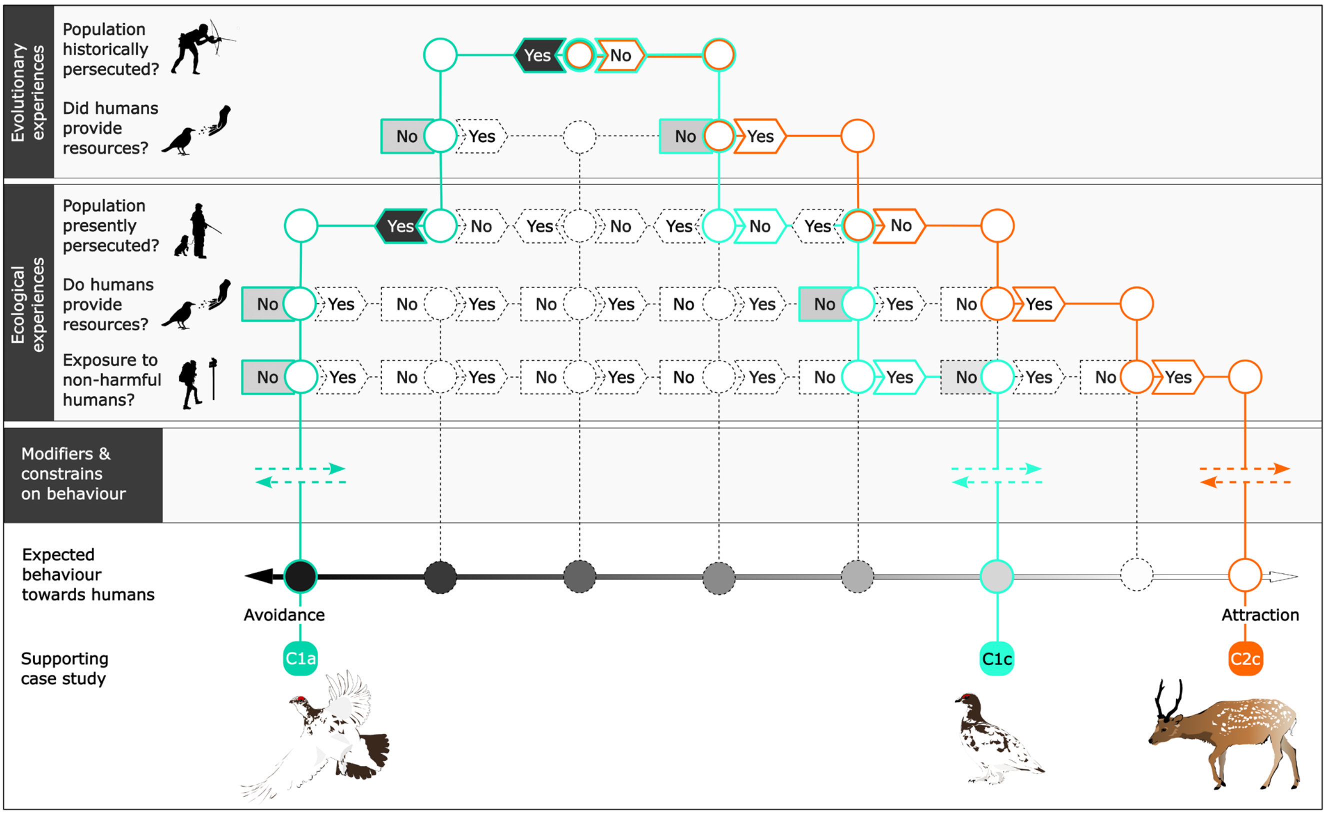
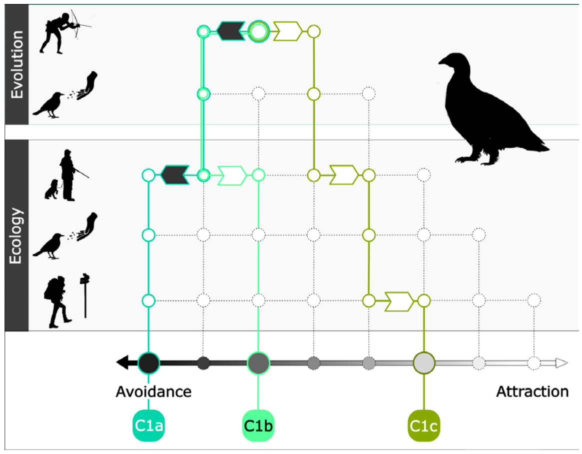
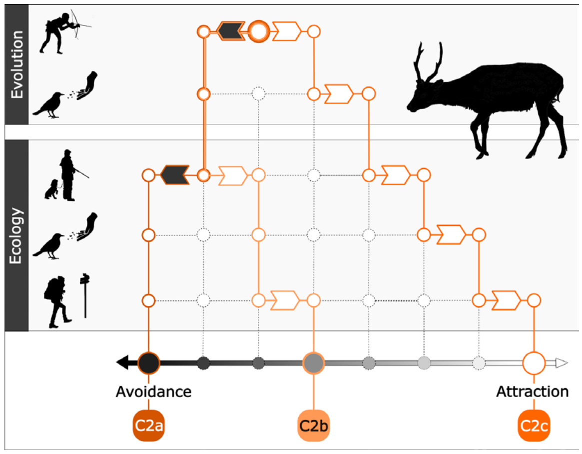
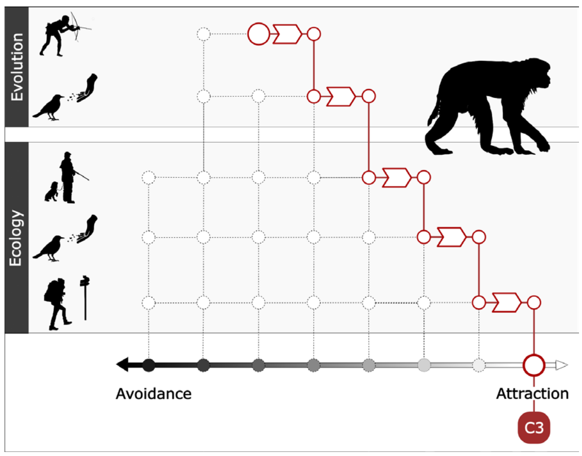


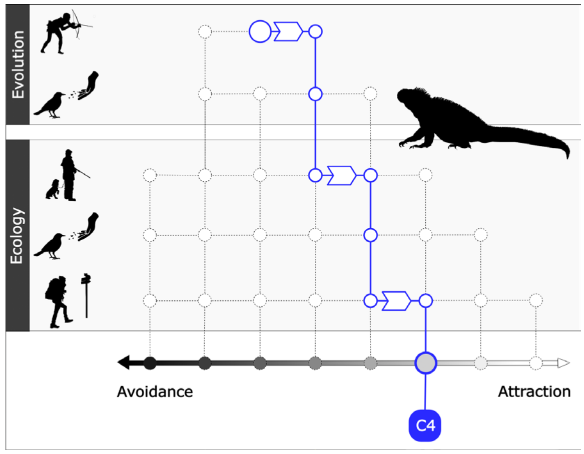
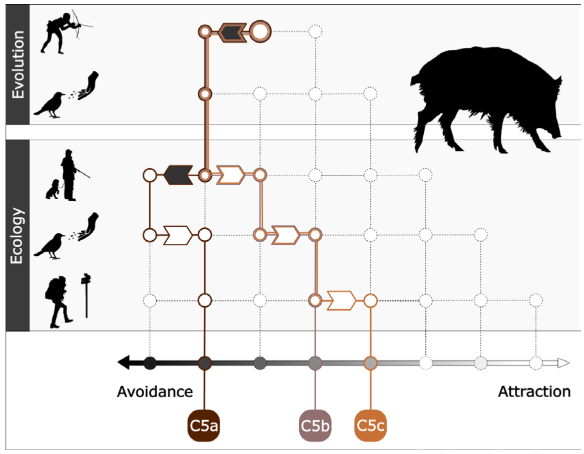
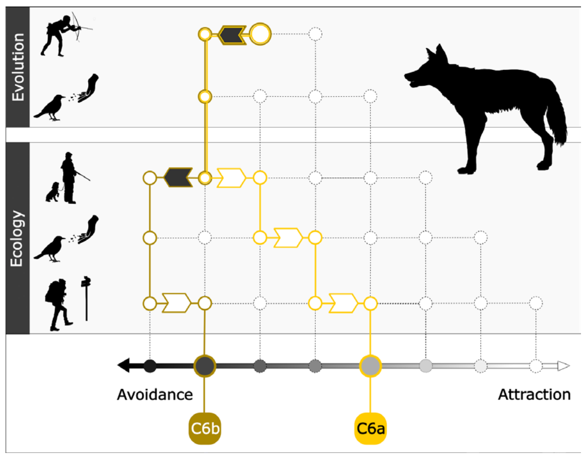
Figure 1. Schematic of the expected shifts of wildlife behavioural responses along the avoidance–attraction continuum shaped by cumulative evolutionary and ecological experiences with humans. Experiences of hunting or persecution are expected to shift behaviour towards avoidance (dark grey arrows pointing left), whereas exposure to benign humans (e.g. non-lethal outdoor recreational activities) and resource-providing humans (e.g. feeding) is predicted to shift behaviour towards attraction (unfilled arrows pointing right). At the continuum centre, expected behavioural responses towards humans are characterized by a high degree of tolerance, without attraction. Scenarios with no expected behavioural shift are shown in light grey boxes. Three of the case studies from Table 1 are exemplified through coloured paths. While presented in a simplified dichotomous format for visualisation, expected behavioural shifts exist on a continuum. For example, the degree of avoidance due to hunting may vary based on intensity and method (direct, such as shooting, versus indirect, such as trapping). Additional modifiers, such as habitat features, physiology, and cognition, may also influence the direction and extent of these behavioural shifts (coloured dashed arrows).

Table 1. Case studies (C) of wildlife behavioural responses to humans along the avoidance–attraction continuum, related to varying evolutionary and ecological experiences with humans. Corresponding diagrams illustrate simplified flows from Fig. 1.

Case study (C)	Corresponding diagram
C1 Rock ptarmigan: *Lagopus muta* are widespread throughout the Alpine and Arctic regions of the Northern Hemisphere and face a variety of avian and mammalian predators, including humans. Ptarmigan hunting has been important in many local cultures and economies. In the European Alps and Iceland, for example, rock ptarmigan flush from humans at greater distances during hunting season, than outside the hunting season. Hunting also appears to have a long-term impact on flushing behaviour, resulting in greater flushing distances in hunted (C1a) compared to non-hunted populations (C1b) even outside the hunting season in Iceland (Sooth et al. in press). Conversely, the Japanese subspecies *L. m. japonica*, which has been protected from hunting due to religious beliefs since ancient times, tolerates humans at close range (Nakamura 2007, 2010; C1c).	
C2 Japanese Sika deer: *Cervus nippon* exhibit the full range of responses to humans along the avoidance–attraction continuum, despite having been hunted historically throughout most of their range. Currently, sika deer are regularly hunted from November to February in most parts of Japan (Takatsuki 2009). Where hunting pressure is high, sika deer respond by reducing use of habitats with high hunting pressure (Ikeda and Koizumi 2024), reducing use of open land during the hunting season (Kamei et al. 2010) and shifting towards nocturnal activity patterns (van Doormaal et al. 2015; C2a). In areas with low or no hunting pressure, sika deer can tolerate human presence, showing little flight from humans in areas with intense recreational use (Borkowski 2001; C2b). Finally, in Nara Deer Park, sika deer have been protected for approximately 1300 years for spiritual reasons, and feeding wild sika deer is a popular attraction. As a result, deer are attracted to humans and coexist in close proximity to humans in extremely dense populations (approximately 226 sika deer per km^2) (Torii and Tatsuzawa 2009, Usui and Funck 2017; C2c).	
C3 Rhesus macaques: *Macaca mulatta* are found throughout most of South and Southeast Asia and often live in and around human settlements and urban areas (Singh et al. 2024). In India, Rhesus macaques have strong religious and cultural connotations – historically, these monkeys have not been hunted or persecuted, and humans offer food to them for religious merits to this day (Radhakrishna 2013, Bisht 2017, Anand et al. 2018). Rhesus macaques are typically attracted to humans rather than shy of them, and monkeys are even known to exploit human resources by stealing food, damaging property, and raiding crops (Beisner et al. 2015, Saraswat et al. 2015). There have been cases of individuals demonstrating aggression towards humans, (e.g. lunging at people, feigned or more rarely realized bites), which is thought to be in response to residents using weapons such as rocks and stones to scare monkeys away from their property, or towards tourist teasing monkeys while feeding them (Radhakrishna and Raman 2016, Bisht 2017, Anand et al. 2018).	

(*Continued*)

Table 1. Continued.

Case study (C)	Corresponding diagram
C4 Galápagos marine iguana: *Amblyrhynchus cristatus*, endemic to the Galápagos Archipelago, have evolved for about 5-15 million years without major predation risk from human and non-human terrestrial predators. Today, the Galápagos marine iguana is protected under Ecuadorian law and listed under CITES Appendix II (MacLeod et al. 2024). Like other endemics on the archipelago, the species is remarkably tolerant to humans, showing little behavioural and physiological responses to humans (Berger et al. 2007, Rödl et al. 2007, Vitousek et al. 2010). This is in contrast to the behaviour and physiological response of iguanas to one of the few native predators of the species, the Galápagos hawk *Buteo galapagoensis* (Vitousek et al. 2010), towards which iguanas do show typical anti-predatory responses.	
C5 Wild boar: *Sus scrofa*, the wild relative of domestic pigs (Evin et al. 2017, Gongora et al. 2017), have historically co-occurred with humans throughout their widespread geographic range. Until present day, wild boar were hunted throughout most of their range. In Germany, where hunting pressure is high, boar are more nocturnal (Johann et al. 2020), flee from humans at longer distances (Wielgus et al. 2024), adjust their habitat utilization patterns based on human activity (Keuling et al. 2018) and show spatial and temporal avoidance of hunting areas (Handschuh et al. 2024, C5a) as compared to non-hunting areas (C5b). This contrast is particularly stark when compared to wild boars in urban areas in Germany, where animals are not hunted and additionally are exposed to high levels of non-lethal human activity (Stillfried et al. 2017, C5c). Similarly, in China, where hunting of wild boar was banned in 1996, boars tend to be attracted to human settlements (Zhao et al. 2019) and are seen rooting through garbage, raiding crops, and entering residential spaces (Wang et al. 2023).	
C6 Coyotes: *Canis latrans*, originally native to the arid, open landscapes of North America, have now considerably expanded their geographical ranges throughout North America (Kays 2018), including human-shaped landscapes and major cities (Thurber and Peterson 1991, Poessel et al. 2017). Since Western-colonialism, coyotes have been persecuted by humans as a pest (Flores 2016), an attitude that prevails to the present day, often rooted in fear of coyote attacks on people and pets, despite the rare frequency with which those occur (White and Gehrt 2009, Mahoney et al. 2018). Coyotes have remarkable behavioural flexibility (Murray and St. Clair 2015, Schell et al. 2018, Young et al. 2019). For example, in urban areas, where coyotes are not typically culled, and often fed by humans, animals show more bold behaviours towards humans (e.g. lower-level flight responses to an approaching person, C6a), as compared to rural areas where coyotes are regularly trapped or shot by private hunters, trappers or wildlife managers (Breck et al. 2019, C6b). Additionally, predator release from mountain lions *Puma concolor* in urban areas may act as modifier, further shifting coyote behaviour towards attraction to humans on the continuum.	

2007, Wund et al. 2015). Accordingly, in systems where humans have historically posed little or no threat to wildlife populations, heritable anti-predator behaviour towards humans should diminish (Coss 1999). Consistent with this, we present several case studies that show variable response of wildlife to humans between populations with or without history of hunting or persecution by humans, including cases within the same species (Table 1: Rock ptarmigan *Lagopus muta* [C1]; Sika deer *Cervus nippon* [C2]; Rhesus macaques *Macaca mulatta* [C3]; Galápagos marine iguana *Amblyrhynchus cristatus* [C4]).

Ecological experience with humans influences wildlife behaviour across the avoidance–attraction continuum

Behaviourally plastic individuals can respond to changing environments throughout their lifetimes, including rapid human-induced alterations (Hendry et al. 2008, Sih et al. 2011, Snell-Rood 2013). For example, despite having been historically persecuted in parts of their range, wild boar *Sus scrofa* and coyotes *Canis latrans* show high levels of tolerance to humans in areas where there is no current persecution (Table 1: C4 and C5). Similarly, rock ptarmigan or Sika deer can show reduced anti-predatory behaviour to humans where hunting pressure is currently alleviated, despite being historically hunted throughout their native ranges (Table 1: C1 and C2). In addition to the case studies presented in Table 1, a variety of species, including mammals, birds, reptiles and fish, have populations that avoid humans when human behaviours pose a risk to animals, such as hunting or culling, but are more tolerant or are attracted to humans when humans are non-threatening and/or feed individuals (e.g. mammals: red deer *Cervus elaphus* Lone et al. 2015, Chassagneux et al. 2019, Alpine marmots *Marmota marmota* Zenth et al. 2025a, Eurasian red squirrels *Sciurus vulgaris* Uchida et al. 2019, 2025, birds: common mynas *Acridotheres tristis* McGiffin et al. 2013, several corvid species Fujioka 2020, reptiles: western fence lizards *Sceloporus occidentalis* Grolle et al. 2014, fish: e.g. northern pike *Esox lucius* Klefoth et al. 2011).

Lifetime experience is an important mechanism for behavioural plasticity, and it may induce epigenetic changes and enable individuals to learn to evaluate stimulus information and adjust (anti-predator) behaviour to prevailing conditions and environmental changes (Mery and Burns 2010, Møller et al. 2015). Two of the most relevant learning processes that shape how wildlife respond to humans are operant conditioning/associative learning – where a behaviour is strengthened or weakened by associated positive or negative consequences, and habituation or sensitisation – non-associative types of learning where the behavioural responses either diminish or strengthen with exposure (Čapkun-Huot et al. 2024). In an anthropogenic context, wildlife may be operantly conditioned to seeking out humans because humans (and/or human settlements) can provide resources (Møller et al. 2015) and safety from predators (human-shield-hypothesis, Berger 2007, Granados et al. 2023). Aversive conditioning, conversely, is often the mechanism behind why animals become more fearful of humans, when being pursued, and is sometimes used in wildlife management, for example to deter animals from conflict areas such as crops (Hsiao et al. 2013), livestock pens (Lorand et al. 2022) or public spaces (Sampson and Van Patter 2020). Importantly, humans do not always behave like other predators (Darimont et al. 2015). Not only do humans kill at higher rates, target adults, healthy individuals, and apex predators, but the associated cues may be relatively novel in the evolutionary history of the species, unreliable and/or dissociated in space or time from the source of immediate danger. This can bias learning and lead to discrepancies between actual risk and exhibited behavioural responses (Darimont et al. 2015, Smith et al. 2021). Elk *Cervus elaphus*, for example, that were hunted with long-range rifles from a distance of several hundred meters, which spatially dissociates the cue and the risk, changed habitat use less than individuals hunted with traditional bow hunting, which required a closer approach of the targeted prey (Thurfjell et al. 2017).

True habituation involves a progressive reduction in response to repeated or continuous stimuli that has neither averse nor beneficial consequences for an animal and should not be confused with attraction (Bejder et al. 2009). Habituation may allow species (even with an evolutionary history of being persecuted or hunted by humans) to develop behavioural tolerance to humans, which can be an adaptive (and sometimes maladaptive) in environments saturated with mostly harmless human-related stimuli (Lowry et al. 2013, Čapkun-Huot et al. 2024). Habituation can also be the reason why deterrent strategies, such as when using noises, fladry or predator-like shapes, can have limited success (Greggor et al. 2020, Bhardwaj et al. 2022). Sensitization, on the other hand, refers to a progressive intensification of behavioural response to a repeated or continuous stimulus that has important consequences for the animal (Bejder et al. 2009). For example, wild bottlenose dolphins *Tursiops truncatus* subjected to commercial swim-with dolphins tourism showed increased avoidance response to swimmers with cumulative swim attempts (Constantine 2001).

Understanding learning mechanisms can provide insights into the underlying mechanisms of behaviours, thus potentially guide management strategies aimed at reducing undesired, and reinforcing desired behaviour (Čapkun-Huot et al. 2024).

Shifting along the continuum: modifiers and constraints to wildlife responses to humans

While the evolutionary and ecological experiences animals have with humans play a role in whether animals display attraction, tolerance, or avoidance of humans, behavioural modulation is complex, involving multiple interrelated factors (Tablado and Jenni 2017, Greggor et al. 2020, Lasky and Bombaci 2023, Čapkun-Huot et al. 2024). Learning is an inherently biased process that can be modified or constrained by perceptual filters, attentional biases and cognitive capacity, among other factors (Greggor et al. 2017). In social species, social learning and/or cultural transmission can additionally trigger, accelerate or bias learning (Heyes 1994). For example, social learning seemed to facilitate habituation to humans in a wild chimpanzee *Pan troglodytes* population where the arrival of two human-tolerant individuals increased the overall tolerance of the previously human-avoidant group (Samuni et al. 2014). Furthermore, learning, and other processes related to behavioural plasticity, can vary consistently among individuals (Dingemanse and Wolf 2013, Stamps 2016). For example, individual yellow-bellied marmots *Marmota flaviventer* differently modified their escape distance in response to repeated human approach over a 15-year period (Uchida and Blumstein 2021). While, on average, marmots decreased their escape distance over time, likely due to habituation-like processes, some individuals that initially fled at greater distances did not habituate, but instead sensitised to repeated approaches, and increased their escape distance over time (Uchida and Blumstein 2021). Likewise, the response of individual black-tailed deer *Odocoileus hemionus sitkensis* to short-term hunting risk is highly correlated to the individual's initial level of tolerance to humans (Le Saout et al. 2014).

In addition to modulators on learning and plasticity, individual behavioural responses to humans may depend on several other factors such as physiology (e.g. sex: Shine et al. 2000, Berger et al. 2007, age: Kalb et al. 2019, nutritional status: Beale and Monaghan 2004, reproductive status: Nellemann et al. 2000 or life history traits: Sol et al. 2018), resource quality: e.g. the extent of investment investments such as nest building or establishment of a territory de Jong et al. 2013, Quadros et al. 2019), or availability of, and distance to, alternative suitable sites: Gill et al. 2001). What may appear as tolerance may be just the lack of other options. For example, during breeding season Adélie penguin *Pygoscelis adeliae* (and other species of penguins) are seemingly tolerant of humans (lack of flight, remain on nest), however, rather than illustrating tolerance to humans, the lack of response may be better explained by the individual's need to remain on their nest to ensure the survival of their chicks that are unable to regulate their body temperature independently (Wilson et al. 1991). The benefit of chick survivorship may be worth the cost of not reacting to human presence, for the penguins in this context. Finally, based on error management theory, in situations of stimulus uncertainty, avoidance may often be the default response, because the costs of a false-negative (i.e. not responding to a threat) are substantially higher than the costs of a false-positive (i.e. mistaking a harmless stimulus for a threat, Johnson et al. 2013). Thus, the avoidance is not driven by an anti-predatory response to humans, per se, but rather an avoidance of any potential risk.

Applying the avoidance–attraction continuum to refine public perception of wildlife behaviour, wildlife management and ecological research

A common public perception is that wildlife should be wild and naturally avoid humans. This may be related to the prevailing view of wildlife and wilderness as something that is natural in a sense of being untrammelled by man (Public Law 88-577 Wilderness Act 1964), and thus somewhat separate from humans and human infrastructure (Cookson 2011, Zoderer et al. 2020). This cognitive bias can influence how public, policymakers and wildlife managers evaluate and respond to wildlife behaviour, particularly when it does not align with preconceived notions. For example, tolerance and attraction to humans, particularly when observed in large carnivores, may be perceived as aberrant behaviour, a priori raising concerns for human safety and, thus, prompting calls for lethal control. However, as we demonstrate, tolerance and attraction are part of the natural spectrum of behavioural responses to humans. This range of responses should be expected in environments that have drastically been changed by human activity (Samia et al. 2015) and should be considered when planning for wildlife management. Moreover, increasingly mutualistic human value orientations toward certain wildlife species can manifest in behaviours such as wildlife feeding or the enactment of protective legislation (Manfredo 2008). Based on our framework, these societal shifts are likely to drive species' behaviours further toward tolerance and attraction, introducing new challenges for coexistence (e.g. recolonising wolves in Europe, Kuijper et al. 2019). Rather than automatically labelling tolerant animals as aberrant, or safety risks, one must carefully assess whether such behaviour actually poses a threat to humans, and under what circumstances. Although tolerance necessarily increases the potential for conflict by enabling greater human–wildlife overlap, studies suggest that often incidents of non-predatory wildlife aggression toward humans result from provocation by humans or situations where animals feel threatened (Linnell et al. 2002, Beisner et al. 2015).

While the negative impacts of human disturbance on wildlife have long been recognized as a serious conservation concern (Ciuti et al. 2012, Storch 2013, Møller et al. 2014, Coetzee and Chown 2016), behavioural tolerance (and attraction) as wildlife management issues, has only recently received attention in the literature (Samia et al. 2015, Uchida et al. 2023, Čapkun-Huot et al. 2024). In particular, recent work has identified habituation and behavioural tolerance towards humans as major mechanism behind why some species (e.g. foxes or racoons in cities) are able to successfully persist in and/or exploit human-shaped habitats (Samia et al. 2015, Bhardwaj et al. 2022, Čapkun-Huot et al. 2024). On the other hand, increased tolerance can have aversive outcomes, such as increased risk of disease transmission between humans and animals, economic damages or aesthetic consequences, for example, when tolerant animals damage crops or gardens, or scatter human litter (Uchida et al. 2023). Increased tolerance to humans may also drive animals into ecological traps, for example, when tolerant animals become more vulnerable to poaching (Kasereka et al. 2006). As human activities and infrastructure continue to encroach into natural habitats, and human–wildlife interactions become more frequent as a result, there is clearly a need for more effective and efficient management strategies to promote conservation while minimizing conflict (Anthony and Blumstein 2000, Berger-Tal et al. 2011, Greggor et al. 2020). A better, nuanced, understanding of animal behaviour along the continuum of avoidance–attraction seems a promising avenue. Wildlife management traditionally relies on wildlife population control to mitigate human–wildlife conflicts (Reidinger and Miller 2013). However, lethal control often clashes with conservation goals and ethical concerns (von Essen and Redmalm 2023), and can be ineffective (Hone 1994, Chapron and Treves 2016, Miller et al. 2016, Swan et al. 2017). In such cases, modifying animal behaviour towards humans (and human spaces) may be effective (Honda et al. 2019, Lorand et al. 2022). For example, conflict with large carnivores, which is often due to depredation of livestock, but also space-sharing and, more rarely, attacks on people, can be effectively mitigated through non-lethal interventions that use aversive conditioning (i.e. teaching animals to associate humans with negative consequences) to increase avoidance towards humans (Rauer et al. 2003, Hawley et al. 2009, Lorand et al. 2022). Aversive conditioning, as a practice, is based in the fact that wildlife has a range of behavioural responses to humans and do not always avoid them. Wildlife managers frequently need to deal with challenges that can arise with habituated wildlife (e.g. ecological, economic or public safety problems, reviewed by Uchida et al. 2023) and there is a growing interest in non-lethal methods to shift wildlife behaviour from tolerance and attraction towards avoidance of humans and/or human spaces (Thompson and Henderson 1998, Kloppers et al. 2005, Found et al. 2018, Petracca et al. 2019, Ogden 2021).

Since attraction to humans is often associated with human–wildlife conflict (Poessel et al. 2013, Priston and McLennan 2013, Can et al. 2014, Nyhus 2016, The Guardian 2024), it is essential to raise awareness about potential attractants/attractive behaviour. In this context, environmental education of citizens about the avoidance–attraction continuum and the role of human behaviour can help foster a better understanding and anticipation of possible behavioural consequences of certain activities such as feeding of wildlife and encourage more responsible behaviour. Conversely, wildlife populations in high-recreational areas experiencing human disturbance may benefit from habituation, which can be facilitated by minimising negative encounters with humans, for example by restricting hunting (Storch 2013, Paton et al. 2017, Kays 2018, Parsons et al. 2022, Fennell et al. 2023, Zenth et al. 2025a). Such management strategies could particularly benefit protected areas such as national parks helping them balance their dual mandate of conserving biodiversity while providing opportunities for the public to experience nature, observe wildlife, and engage in environmental education.

Considering wildlife behaviour along the avoidance–attraction continuum can improve effective non-lethal management strategies; however, there are key research questions that remain to be explored. Relevant questions include the intensity and frequency of aversive/neutral stimuli needed to sensitise/habituate wildlife to humans (Blumstein 2016) or the possibility of modifying the behaviour of species or populations with strong historical experiences with humans. This could be explored by explicitly altering human behaviour towards a population, to elicit if, and how, the population modifies its behaviour over time. Another key gap in knowledge is how contrasting experiences with humans shape wildlife's perception of risk (Colman et al. 2001, Courbin et al. 2022, Mols et al. 2022). For instance, Rhesus macaques *Macaca mulatta* in India tolerate close human presence due to food provisioning, but teasing by humans often triggers aggression in both animals and people (Table 1: C3). Elucidating such dynamics would require studies that compare wildlife behaviour towards humans in areas with and without hunting (or other forms of persecution), while considering potential interactions between protection regimes and varying levels of exposure to non-harmful human activities, such as outdoor recreation. While our focus here is on wildlife behavioural responses to the presence of humans, wildlife may also respond behaviourally to human-shaped landscapes and infrastructure. Such responses often manifest as temporal or spatial shifts in presence or habitat use, reflecting ecological tradeoffs (Nickel et al. 2020, Handschuh et al. 2024). For example, wildlife may be attracted to humans per se in cases where animals are hand-feed, but could also be attracted to resources associated with humans while simultaneously avoiding human presence (e.g. leopards *Panthera uncia* in Mumbai: Surve et al. 2022). Continued research is needed to investigate the relationship between the behavioural response of wildlife to human presence and landscape modification by humans.

Besides its relevance for conservation and other management contexts, the assumption that humans are generally perceived as predators in human–wildlife interactions, and thus that avoidance is the default response, can bias research by influencing study design and interpretation of results. For example, quantifying the wariness of individuals towards non-human threats as measured by the distance at which individuals flee from an approaching human (Rödl et al. 2007), is likely not accurate in all systems and may lead to misinterpretation of results (Coleman et al. 2008). It has been shown in several species that individuals are able to differentially assess risk levels, such as in Eurasian red squirrels, in which urban-dwelling individuals have reduced escape distances to humans and non-human predator models, but not to novel objects, suggesting that these animals are able to differentially assess risk levels (Uchida et al. 2019). Additionally, habitat suitability models, species distribution models, and other models that predict wildlife occurrence, are often based on the assumption that wildlife generally perceive areas with high human activity as risky (Corradini et al. 2021, Lucas et al. 2023). However, this assumption, may not hold across all species and contexts, limiting their predictability and projections for new areas and populations. For example, several meta-analyses encompassing sub-studies across varied ecological contexts and populations have yielded mixed evidence regarding commonly held ecological assumptions on the behaviour of wildlife towards humans, thus illustrating the variability in response to humans (e.g. human-shield-hypothesis: Granados et al. 2023, Gaynor et al. 2025, wildlife responses to the COVID-19 'anthropause': Burton et al. 2024, diel activity patterns: Devarajan et al. 2025). By appreciating the variety of expected response of wildlife to humans, that extends beyond avoidance, and account for the ability of individuals to learn or demonstrate behavioural plasticity, we can design better balanced studies and may improve our ability to predict the outcomes of human–wildlife interactions.

Conclusion

Evolutionary and ecological experiences with humans shape how wildlife responds to human activity. A growing body of literature suggests that humans are not always 'super predators', and we suggested that better appreciation of the full range of wildlife responses towards humans along a continuum of avoidance–attraction is needed in research, conservation and wildlife management. We emphasized the need to account for the historical and current context of human–wildlife interactions to better understand and predict how wildlife will respond to human activity, whether that be avoidance, tolerance or attraction. Understanding the complex nuanced relationships between humans and wildlife, rather than simplifying and/or assuming outcomes, is essential to the continual development of our knowledge of human–wildlife systems, and fostering successful coexistence between humans and wildlife in the Anthropocene.

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Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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