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REVIEW

Contemporary Methods for Studying Animal Sociality in the Wild

Disgust in animals and the application of disease avoidance to wildlife management and conservation

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Abstract

1. Disgust is an adaptive system hypothesized to have evolved to reduce the risk of becoming sick. It is associated with behavioural, cognitive and physiological responses tuned to allow animals to avoid and/or get rid of parasites, pathogens and toxins.
2. Little is known about the mechanisms and outcomes of disease avoidance in wild animals. Furthermore, given the escalation of negative human-wildlife interactions, the translation of such knowledge into the design of evolutionarily relevant conservation and wildlife management strategies is becoming urgent.
3. Contemporary methods in animal ecology and related fields, using direct (sensory cues) or indirect (remote sensing technologies and machine learning) means, provide a flexible toolbox for testing and applying disgust at individual and collective levels.
4. In this review/perspective paper, we provide an empirical framework for testing the adaptive function of disgust and its associated disease avoidance behaviours across species, from the least to the most social, in different habitats. We predict various trade-offs to be at play depending on the social system and ecology of the species.
5. We propose five contexts in which disgust-related avoidance behaviours could be applied, including endangered species rehabilitation, invasive species, crop-raiding, urban pests and animal tourism.
6. We highlight some of the perspectives and current challenges of testing disgust in the wild. In particular, we recommend future studies to consider together disease, predation and competition risks. We discuss the ethics associated with disgust

experiments in the above contexts. Finally, we promote the creation of a database gathering disease avoidance evidence in animals and its applications.

KEYWORDS
behavioural immunity, ecological niches, field experiments, landscape of disgust, pathogen avoidance, sensory aversion, social systems

1 | INTRODUCTION

1.1 | Into the wild: Eat and be eaten

Animals have evolved with selective pressures such as disease and predation that have shaped their morphology, physiology, behaviour and ecology. Consider the maxillary overhang (the tip of the upper beak curving beyond the lower mandible) that some bird species exhibit. The longer the overhang, the better individuals are at removing lice during preening (Moyer et al., 2002). When morphology does not allow for defence against parasites or predators, and when behaviour (see below) supersedes the costs of a constitutive defence, physiology can play a predominant role. For instance, ground squirrels (*Otospermophilus* spp.) that share an evolutionary history with viperid snakes show resistance to their venom (Biardi et al., 2006). Other species have evolved extreme behavioural adaptations to get rid of parasites. When infected with internal parasitic copepods (*Arthurius* sp.), the sea slug *Elysia atroviridis* self-decapitate and regrow a new body free of parasites (Mitoh & Yusa, 2021). Beyond individuals, parasites can also shape ecological communities. A mange *Sarcoptes scabiei* outbreak in 2015 in Argentina's San Guillermo National Park killed most of the vicuña *Vicugna vicugna* population, a mammalian herbivore foraging in meadows during the day to avoid its predator, the puma *Puma concolour*. Consequently, plant biomass, cover and height increased in meadows, homogenizing the landscape. Less prey were available for the pumas, and thus few carcasses were left for the Andean condors *Vultur gryphus* after the early stages of the outbreak. This led the vulnerable condors to significantly reduce their use of the protected area (Monk et al., 2022).

The existing literature contains far more examples of prey–predator than host–parasite interactions (Raffel et al., 2008). The ecology of fear (Brown et al., 1999) was conceptualized much earlier than the ecology of disgust (Buck et al., 2018; Weinstein et al., 2018), or more generally the ecology of peril, which accounts for both perceived predation and disease risks (Doherty & Ruehle, 2020). Even in disciplines that interplay with animal ecology, such as cognitive sciences and conservation biology (Dominoni et al., 2020; Real, 1993), predator avoidance is considered far more often than parasite avoidance (Griffin et al., 2000; Mettke-Hofmann, 2014; Szabo et al., 2022). This discrepancy may be due to a size difference between predators (generally larger than their prey) and parasites (usually smaller than their hosts), but also to differences in outcomes: instant death vs. fitness reduction or slower death (in the case of lethal pathogens; Box 1). For instance, 15 years of mortality data in southern sea otters *Enhydra lutris nereis* show that the primary cause of death was white shark *Carcharodon carcharias* bite (28%). However, when considering primary and contributing causes of death together, pathogens provoked the highest death rates (63%; Miller et al., 2020). Greater energy is thus allocated to avoiding more lethal natural enemies such as predators and some of the more dangerous parasites, than non-lethal ones (Buck et al., 2018; Doherty & Ruehle, 2020).

BOX 1 Glossary

Parasite: any organism that lives in or on another organism (its host) and gets food from or at its host's expense (i.e. endoparasite, ectoparasite).

Pathogen: organism that causes disease (i.e. bacterium, virus, protozoan, fungus, worm).

Toxin: poisonous substance produced by living cells or organisms capable of causing disease or death (e.g. plant alkaloid).

Contaminant: biological or chemical substance containing infectious agents or poisons/toxins (e.g. faeces, heavy metal).

1.2 | Avoidance, resistance, tolerance or the ART of pathogen handling

Just as predators employ different strategies to capture their prey (i.e. ambush, interception and pursuit), parasites and pathogens use different pathways to infect their hosts (e.g. faecal-oral, trophic, respiratory)—which imply numerous trade-offs (Antonovics et al., 2017). Hosts have evolved three strategies to defend themselves against parasites, pathogens and toxins: avoidance, resistance and tolerance (ART; Rivas et al., 2014). As defined by Rivas et al. (2014), ART calls on distinct immune systems interacting with each other (see Schaller et al., 2010 and "*Disgust*" below): the behavioural immune system prompting avoidance and removal (Amoroso & Antonovics, 2020; Schaller & Park, 2011), and the physiological immune system underlying resistance and tolerance (Figure 1).

In this paper, we focus on behaviours as these are the frontline defences against parasites and pathogens (Sarabian, Curtis, & McMullan, 2018). We propose to adapt the ART framework to better encapsulate the variation in (and levels of) behavioural immunity, based on the type (endo- vs. ecto-), timing (before vs. after), severity

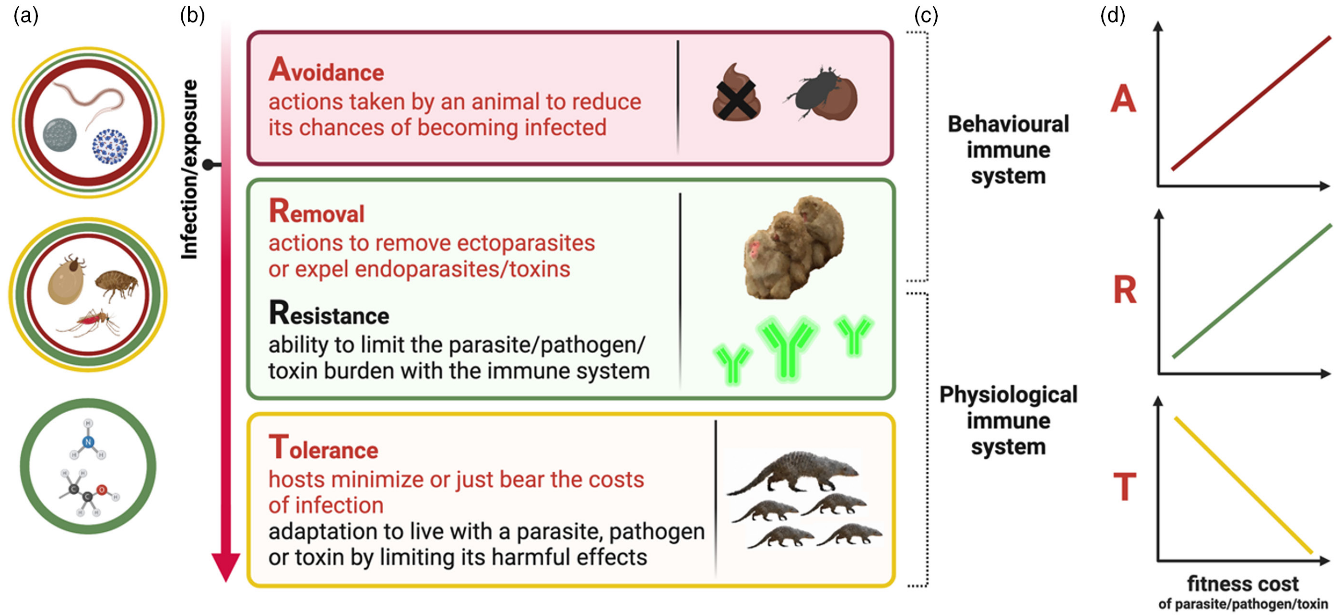

FIGURE 1 The ART of immunity. (a) Organisms and molecules capable of damaging hosts' fitness, from top to bottom: endoparasites, which can be pathogens; ectoparasites and toxins. The colour and width of the circle reflect the main strategy (avoidance: red; removal: green; tolerance: yellow) predicted to be used by the hosts to handle these threats when detected. Note that for lethal biotoxins produced by predators or by prey toward predators, the main strategy would be the avoidance of the conspicuous signs associated with these animals (not represented in this model). (b) Part of the ART framework intervenes before (i.e. avoidance) and the other part after infection or exposure (i.e. removal/resistance and tolerance). The behavioural components of ART are written in red and illustrated with examples found in the main text (A: avoidance of pathogenic bacteria in dung beetles; R: lice picking in Japanese macaques; T: acceptation of visibly diseased group members in banded mongooses). (c) Avoidance and removal call upon the behavioural immune system while tolerance mainly involves the physiological immune system (along with behaviours that may compensate infection). (d) ART investment based on fitness costs: while avoidance and removal may increase with the fitness cost of the parasite, pathogen or toxin, tolerance is expected to decrease. Created with BioRender.

of the fitness cost, and ecological context of infection/exposure/intoxication (Figure 1). As such, *avoidance* occurs when parasites/pathogens are detected through species-specific sensory modalities before infection and when the cost of the behavioural action is lower than the cost of acquiring the infection, or in other words net-beneficial (see Oliva-Vidal et al., 2021; Table S1). For instance, by avoiding faeces altogether in a feeding context and not being discriminatory between fresh and old ones, mandrills *Mandrillus sphinx* can evade a large array of faecally-borne parasites with different life cycles (Poirotte et al., 2019).

Removal happens once a parasite has been acquired, and when the behavioural action does not exceed the cost of infection. For instance, preening or grooming is regularly used by numerous species of birds and mammals to remove lice and ticks, as well as to maintain social bonds when performed in a social context (Bush & Clayton, 2018; Henazi & Barrett, 1999). Self-medication is a case of removal, as it can help expel gastrointestinal parasites and treat or prevent skin disease via either the ingestion or cutaneous application of plant secondary metabolites or arthropod toxins (Clayton & Wolfe, 1993; Morrogh-Bernard et al., 2017).

Finally, *tolerance* happens when hosts minimize or just bear the costs of infection rather than aiming to eliminate the parasites/pathogens altogether. For instance, banded mongooses *Mungos mungo* do not avoid conspecifics infected with *Mycobacterium mungi*, a causative agent of tuberculosis that manifests as nasal swelling and skin lesions in these animals. This lack of avoidance is perhaps due to their highly cohesive social system, which would not allow the survival of isolated individuals and thus ultimately promotes equal exposure among the colony (Fairbanks et al., 2015). Alternatively, close social bonds or responsibilities, such as those seen between mother-offspring dyads, might suppress avoidance behaviour and promote tolerance, as shown in vampire bats *Desmodus rotundus* (Stockmaier et al., 2020) and mandrills (Poirotte & Charpentier, 2020). Among the three strategies for dealing with parasite threats, however, avoidance is likely the most cost-effective as it offers a direct means of prevention.

2 | DISGUST: A SCULPTURE OF EVOLUTION TO PREVENT INFECTION

What triggers avoidance? One hypothesis is that disgust, an adaptive system based in neural tissue (*Homo sapiens*: Phillips et al., 1997; *Macaca mulatta*: Caruana et al., 2011; *Mus musculus*: Dolensek et al., 2020), evolved to detect cues that co-occur with parasites, pathogens and toxins and instigate behavioural, cognitive and physiological responses that reduce the risk of getting sick (Curtis et al., 2011; Curtis & Biran, 2001; Kavaliers et al., 2021; Oaten et al., 2009; Tybur

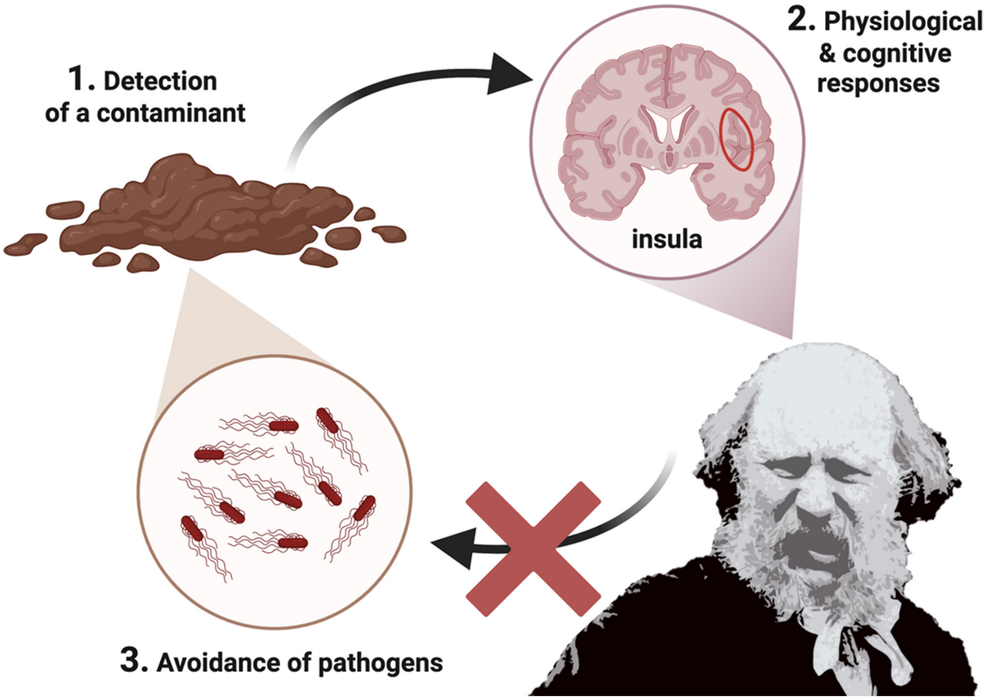

FIGURE 2 The adaptive system of disgust. An animal (host) detects sensory cues that co-occur with parasites, pathogens (e.g. faeces) and/or toxins—which instigates physiological (e.g. activation of the insula in humans, macaques and mice), cognitive and behavioural (e.g. pathogen avoidance) responses reducing the risk of disease. Created with BioRender. Darwin's expression of disgust was modified from the original image under a Creative Commons licence.

et al., 2013; Figure 2). For instance, female western lowland gorillas *Gorilla gorilla gorilla* are likely to leave their group when other members or the mature male ("silverback") present severe facial skin lesions caused by a *Treponema* bacterium (Baudouin et al., 2019). Similarly, *Caenorhabditis elegans* (302-neuron-1-millimetre-long nematodes) move away from pathogenic bacteria when placed together in a Petri dish (Pradel et al., 2007). Even coprophagic dung beetles *Scarabaeus* (*Kheper*) *lamarcki* will not approach carnivore faeces due to a volatile compound (phenol) produced by pathogenic bacteria decomposing proteins therein (Mansourian et al., 2016).

Besides visual and olfactory cues, healthy subjects can also receive warnings via sensory cues that require contact with the contaminant. Newborns of several species, including rats *Rattus norvegicus* (albino Sabra strain), chimpanzees *Pan troglodytes*, gorillas, orangutans *Pongo pygmaeus*, humans and other primates, express behaviours that appear aimed at expelling toxins out of the mouth (Rozin et al., 2008) such as the downward protrusion of the tongue, gaping and/or grimacing after tasting quinine (a bitter-tasting alkaloid found in the bark of cinchona trees; Ganchrow et al., 1983; Steiner et al., 2001). Another example is instant hand removal after touching invisible soft and moist substrates, physical conditions that favour pathogen development (humans: Oum et al., 2011; chimpanzees: Sarabian et al., 2017). Perceived stickiness and adhesiveness may also trigger post-contact hygienic behaviours such as hand washing in humans (Saluja & Stevenson, 2022), penis wiping (with leaves) in chimpanzees (O'Hara & Lee, 2006), and food processing (rubbing, rolling, and washing) in macaques (*Macaca fuscata*: Sarabian & MacIntosh, 2015; *Macaca fascicularis*: Sarabian et al., 2020). Disgust can be divided into several domains based on the route of parasite/pathogen (and toxin) transmission (Tybur et al., 2009, 2013), its elicitors (Amoroso et al., 2019) and the different actions to avoid them (Curtis & de Barra, 2018). Kupfer et al. (2021) propose two main components: the gut defence system—to which the examples above and the proposed framework below refer—and the skin defence system directed toward ectoparasites, which needs further investigation.

Disgust not only influences behaviour across differing scales, from individual facial expressions (Darwin, 2015; Ekman et al., 1992) to the collective decisions of groups (see above; Table S1), but may also affect animal cognition. Several studies conducted with human subjects show that we are slower in discriminating shapes when exposed to disgusting images (e.g. of cockroaches) compared to neutral and fear images (Chapman et al., 2013; Krusemark & Li, 2011), and that we better recall disgusting images compared to scary or neutral ones (Moeck et al., 2021). Recent findings in chimpanzees also show that repeated exposure to disgust-related images (Haberkamp et al., 2017) diminish their performance in a number ordering task (Sarabian, MacIntosh, & Adachi, 2021); they perform the task faster after displays of snake images but slower after carcass images (of non-primates) compared to control mosaic images (Cécile Sarabian, unpublished data). After an initial attentional bias during information processing (Perone et al., 2021), disgust-related images elicit gaze avoidance in humans (e.g. Armstrong et al., 2014), which may prime the body to escape infection. A similar process in chimpanzees may alter their focus on the task and reduce their performance (Sarabian, MacIntosh, & Adachi, 2021). Replication studies are now needed in species that have different psychological and neurobiological architectures.

Just as the body will respond immunologically to fear by preparing for injury or attack (see Maier & Watkins, 1998), disgust initiates physiological immune responses to prepare the body for infection (Schaller et al., 2010). For instance, people exposed to images indicative of pathogen presence increase their level of cytokines involved in the inflammatory process that clears infection (Schaller et al., 2010; Stevenson et al., 2011). Physiological immune responses may be particularly helpful when behaviour and cognition are constrained by other factors such as nutrition (Sarabian & MacIntosh, 2015), parental care (Case et al., 2006; Poirotte & Charpentier, 2020; Stockmaier et al., 2020), reproduction (Paciência et al., 2019) or limited space. When exposed to lethargic conspecifics infected with *Mycoplasma gallisepticum* (provoking chronic respiratory disease or conjunctivitis in birds), caged domestic canaries *Serinus canaria domestica* increased neutrophils in their bloodstream, synonymous with an activated physiological immune system (Love et al., 2021). What these trade-offs also point at is the individual and environmental variability in pathogen (disgust) sensitivity, leading to different health outcomes. State-of-the-art research in primates show that the more hygienic/disgust-sensitive individuals are, the fewer infections (intensity or richness) they have (Japanese macaques: Sarabian & MacIntosh, 2015; grey mouse lemurs *Microcebus murinus*: Poirotte & Kappeler, 2019; bonobos *Pan paniscus*: Sarabian, Belais, & MacIntosh, 2021; humans: Cepon-Robins et al., 2021).

The preventive function of disgust seems evident from the literature and the examples given above, but the likelihood that disgust also acts to communicate risk is a crucial aspect that has received little attention outside of the laboratory. Recognition of a 'disgusted' individual would confer a selective advantage to the perceivers of such signals or cues. In mammals, this can translate into the activation of facial muscles. For instance, humans, macaques and mice wrinkle the nose, narrow the eyes and raise the upper lip (Caruana et al., 2011; Dolensek et al., 2020; Ekman et al., 2002), which may benefit the emitter by restricting exposure to sensory cues but also viewers by communicating a potential pathogen threat. These facial expressions can be innate or learnt depending on the pathogenicity/toxicity of the elicitor (Dolensek et al., 2020; Soussignan et al., 1997). Beyond mammals, other species can learn what not to eat by attending to conspecifics distaste response. Birds experiencing unpalatable food (i.e. with toxin) would shake their head, wipe their bill and gape (Sherwin et al., 2002; Thorogood et al., 2018). In most cases, conspecific observers avoid eating the food associated with these behavioural signs (domestic hen *Gallus gallus domesticus* chicks: Johnston et al., 1998; great tits *Parus major*: Hämäläinen et al., 2019, 2020), but see Sherwin et al. (2002) for adult hens, which did not. Investigating such traits in other species, whether at a 'micro-facial' scale or at a larger behavioural or ecological scale is essential for understanding social transmission of this information (Box 2).

BOX 2 Key questions regarding the social transmission of disgust

- What signals (i.e. features that have the function of communicating information) might be transmitted and perceived?
- Who is the signaller and the receiver?
- What role does social and/or associative learning play in any subsequent avoidance behaviours (see Turcsán et al., 2015)?
- Do solitary species lack such signals and/or are they less sensitive to them?
- Can states of disgust be transmitted across species—as fear can (Adolphs, 2013)?
- What might be the ecological consequences of an interspecific spread of disgust states?

In sum, parasite avoidance and disgust involve innate and/or learnt behaviours that evolved in the context of the ecology and social lives of different species (Buck et al., 2018; Curtis, 2014; Kavaliers et al., 2021).

2.1 | Moving beyond model species and lab experiments

Most studies exploring the behavioural components of disgust have been performed in a controlled environment with a few model taxa: social insects (Cremer et al., 2007); fish (Behringer et al., 2018); ungulates (Coulson et al., 2018); rodents (Kavaliers et al., 2021); and humans (Tybur et al., 2014). Yet, disgust is gaining more attention in the fields of ecology and animal behaviour. Weinstein et al. (2018) pioneered a theoretical framework examining the role of the adaptive system of disgust and its associated parasite avoidance behaviours (in addition to predator avoidance; Laundre et al., 2010) in shaping ecosystems. However, empirical evidence of parasite avoidance in the wild is mainly limited to certain taxa and species at individual and group levels of ecological organization (Buck et al., 2018; Sarabian, Curtis, & McMullan, 2018). While strategies to prevent infection may be restricted to or at least dominated by screening food and substrates for contamination in solitary species, group-living species may additionally need to avoid infected conspecifics and their 'byproducts' (Table S1). For example, recent studies on the avoidance of dead carnivores by carnivores support the infection risk reduction hypothesis (Gonzálvez, Martínez-Carrasco, & Moleón, 2021; Gonzálvez, Martínez-Carrasco, Sánchez-Zapata, et al., 2021; Moleón et al., 2017; Oliva-Vidal et al., 2021). Studying the behavioural components of disgust in a wider panel of species in their natural environment and/or in relevant contexts could provide valuable information that may have direct applications to their conservation in the wild (see below).

2.2 | Potential applications of disgust

Most methods used in wildlife management and conservation are based on human needs without considering the adaptive behavioural strategies of the targeted species (Berger-Tal et al., 2016; Khorozyan & Waltert, 2021; Mumby & Plotnik, 2018). Cost-effective deterrence methods based on fear and disgust (although not labelled as such) have been used to mitigate negative human-wildlife interactions in a few instances. For example, anti-predator signals (e.g. eyespots, illness-associated smells/tastes) reduce predation from carnivores on livestock, eggs and endangered species (Radford et al., 2020; Snijders et al., 2021; Tobajas, Descalzo, et al., 2020). Felid growls and beehives reduce crop-raiding by elephants (*Elephas maximus*: Thuppil & Coss, 2016; *Loxodonta africana*: King et al., 2017). Besides conditioned-taste aversion (CTA; see below), a type of learning which allows an individual to rapidly form an association between illness (e.g. nausea) and a particular taste or food item (Snijders et al., 2021), disgust applications in conservation are scarce. The ecology of disgust is still in its infancy and transitioning from theory to practice is challenging. However, based on the growing literature about parasite avoidance in nature (Table S1) and the efficient use of disgust in public health (Biran et al., 2014; Curtis, 2011) and consumer behaviour (Powell, 2021), we propose five contexts, with examples of species, in which disgust-related avoidance behaviours could be further applied. These include endangered species reintroduction and survival, invasive species, crop-raiding, urban pests and animal tourism.

3 | CONTEMPORARY METHODS TO STUDY DISGUST IN THE WILD

The study of avoidance behaviours in wildlife mainly used pathogen-related visual and/or olfactory cues (see Table S1). These sensory cues were adapted to the host–parasite/pathogen systems tested but also denote the absence of investigation in taxa relying primarily on chemosensory and haptic modalities such as reptiles (e.g. crocodilians, snakes) and molluscs (e.g. cephalopods). Below, we provide examples of direct (via sensory cues) and indirect (via computer and machine learning) methods that can be applied to the study of disgust in wild animals (Figure 3).

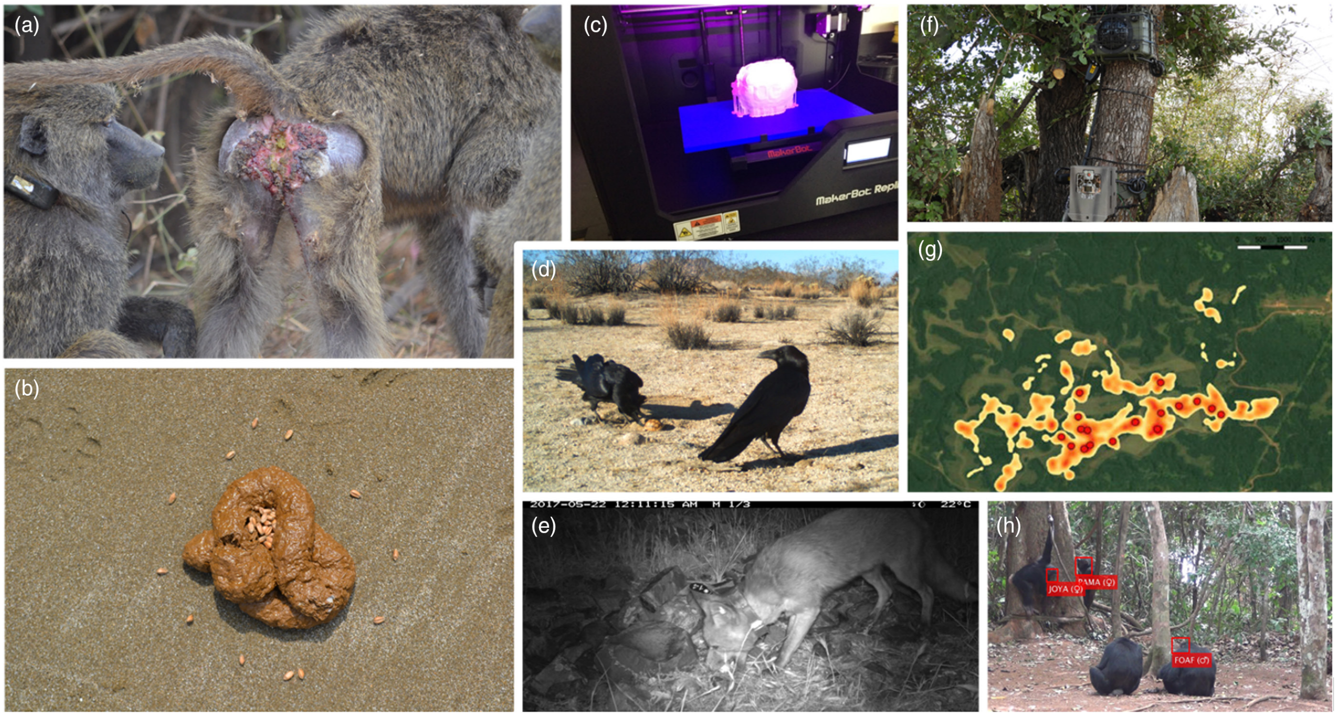

FIGURE 3 Examples of direct (a–f) and indirect (g, h) methods to study disgust in wild animals. (a) Olive baboon exposed to a *Treponema*-infected conspecific and its symptoms. (b) Replica faeces presented to Japanese macaques. (c, d) 3D printed and painted Mojave desert tortoise *Gopherus agassizii* (Techno-tortoise™) filled with an aversive substance to lure predators (ravens) and induce conditioned food aversion. (e) Free ranging red fox *Vulpes vulpes* eating an aversive treated egg to protect ground-nesting birds. (f) Automated Behavioural Response system that could be used to display sounds of sickness when animals pass by. (g) Higher utilization of sites (red) in mandrills negatively correlates with faecal contamination. (h) Chimpanzee face recognition via deep learning. Photo credits (from a to h): Filipa M. D. Paciência; Cécile Sarabian; Tim Shields/Hardshell Labs; Michael Clinchy; Jorge Tobajas; Clémence Poirotte; The Bossou Archive Project of Kyoto University/Daniel Schofield.

3.1 | Artificial contaminants and conspecifics

One way to trigger disgust in animals is to reproduce what can make them sick. These replicas can concern biological contaminants with which contact should be avoided or sick conspecifics from whom distance should be maintained. Previous experimental studies in the field and in different captive conditions have tested whether replica faeces deter primates from foraging (Figure 3b). Individuals either fed significantly less on top of replica (Japanese macaques: Sarabian & MacIntosh, 2015; mandrills: Sarabian et al., 2020), prioritized food on top of control substrates (chimpanzees: Sarabian et al., 2017) or investigated and processed the 'contaminated' food before eating (Japanese macaques: Sarabian & MacIntosh, 2015; long-tailed macaques: Sarabian et al., 2020). Besides visuals, olfactory cues of biological contaminants can be isolated or reproduced and tested. Surfaces impregnated with rotten fruit, rotten meat or faeces odours, for example, elicit significantly less contacts from bonobos than control odours (Sarabian, Belais, MacIntosh, 2018a). Another method to mimic biological contaminants consists in replicating their texture. After touching an invisible soft and moist piece of dough, only half of the chimpanzees tested ate the valued banana reward, against most of them after touching the solid and dry control rope (Sarabian et al., 2017). Taken together, these results highlight the importance of visual, olfactory and tactile cues in contaminant recognition and avoidance in primates. Future field studies could gather all sensory cues associated with disease risk in one artificial contaminant.

An alternative or complementary way to simulate disease risk is to replicate sick or non-hygienic conspecifics using different sensory modalities (Figure 3a). To our knowledge, this approach has been restricted to a few taxa in captivity by adding artifices to healthy individuals. Female captive sage grouse *Centrocercus urophasianus*, for instance, avoid males with artificial haematomas supposed to resemble those created by lice (Spurrier et al., 1991). The use of artificial animals or their byproducts (e.g. eggs) in animal behaviour research is nonetheless increasing, both in the lab and the field (e.g. Frohnwieser et al., 2019; Hauber et al., 2021; Le Maho et al., 2014). Realistic and interactive models are created with the use of novel technologies such as 3D printing (Figure 3c). Models could be adapted to display visual or olfactory cues of disease, for example yaws-like facial skin lesions in an infant gorilla, and observe the proportion of contacts, the number of positive and negative interactions, and so forth by other group members (compared to a control model). Artificial models can also be used in aversion studies to protect endangered species from invasive ones (e.g. Techno-tortoise™, Hardshell Labs; Figure 3d) or to test aversion toward conspecifics or prey (see 4.). Responses to artificial conspecifics could then be compared across species with different social systems to test the potential differences or convergences in behavioural immunity. Although artificial models can be recognized as not being true conspecifics after sensory investigations, the initial phases of interactions can still provide valuable information.

3.2 | Playback experiments

The use of acoustic cues to study disgust and pathogen avoidance is limited to humans in the lab (Michalak et al., 2020; Speed et al., 2021). This is perhaps due to the challenge of identifying and recording relevant sounds of sickness in animals. If available, such cues (e.g. cough, sneeze, diarrhoea) could be added to artificial conspecifics or their byproducts (see above) along with visual, haptic and/or olfactory ones (e.g. mucus on the nose, brown sticky substance on the hindquarters, butyric acid to replicate the odour of vomit). Such playback experiments could be implemented via an Automated Behavioural Response system (i.e camera trap system with speaker that displays programmed sounds when an animal is detected; Suraci et al., 2017; Figure 3f).

3.3 | Conditioned-taste aversion

Testing disgust via taste in the field may be more challenging due to the nature of the cue, which requires mouth contact with or ingestion of a toxic substance. Depending on the field site and the species tested (whether considered a pest or not and neophobic or not), this type of invasive experiment may nonetheless be possible with sufficient welfare assessment (Smith et al., 2022). Lab experiments with rats and other rodents show that taste aversion, in comparison to taste avoidance, induces disgust-associated responses such as nausea and gaping (Parker, 2003; Schier et al., 2019). CTA experiments in the field do not necessarily consider the relation of taste aversion with disgust but rather focus on its applications to mitigate human-wildlife conflicts (Snijders et al., 2021). The method uses illness inducing substances in or on target food/substrates with a variety of species involved in these conflicts to reduce their consummatory behaviours. Successful field experiments show a reduction of egg predation (Figure 3e), toxic species/bait consumption and valued species depredation (Snijders et al., 2021). These experiments often combine illness-inducing toxins with other sensory cues (i.e. visual or odour) during the conditioning phase, and show that the sensory cue alone in the post-conditioning phase is enough to induce aversion (Dimmick & Nicolaus, 1990; Tobajas, Ruiz-Aguilera, et al., 2020).

3.4 | Remote sensing technologies

Bio-loggers are increasingly used in ecological studies (Fehlmann & King, 2016), most of the time attached to the animals (Wilmers et al., 2015), but also to food (see below) or tools (Katarina Almeida-Warren, unpubl. data) and thus help in the monitoring of animal behaviour. The cascading effects of disgust at a landscape level have not yet been empirically assessed (Weinstein et al., 2018), however, recent studies show the possibility of doing so. Gálvez and Hernández (2022), for example, placed tagged seeds and camera traps next to ocelot *Leopardus pardalis* urine and faeces and found a lower rate of seed dispersal by agoutis *Dasyprocta punctata* under simulated predation risk. One could replace ocelot faeces and urine by non-predator faeces (of conspecifics or other rodents from which parasites/pathogens can be acquired) and test whether such cues also affect agoutis' seed dispersal and landscape use. Using handheld GPS devices, Poirotte et al. (2019) recorded mandrill ranging behaviour in the rainforest and showed less frequent returning to sites highly contaminated by conspecific faeces compared to sites with lower contamination levels (Figure 3g). One could next investigate how such movement patterns linked to contamination affect interspecies interactions at different trophic levels.

3.5 | Artificial intelligence

Disgust-related avoidance behaviours could be automatically tracked/detected via machine learning (developed algorithms) based on images collected by video/drone, camera trap or other types of devices. Depending on the scale of the images or footages (e.g. aerial view, individual focus), the processing can answer different questions related to landscape use, body movements, social networks, or facial expressions to assess pathogen avoidance at an individual or collective level. For example, deep-convolutional neural network models can individually recognize dozens of individuals from video footage and allow social network analysis based on co-occurrences of identified individuals in video frames (Schofield et al., 2019; Figure 3h). DeepPoseKit (Graving et al., 2019) and DeepLabCut (Mathis et al., 2018) are software packages that allow pose estimation on the animal body and could automatically track body features such as the camouflaging of an octopus, the facial muscle activation of a primate or the head retraction of a turtle—behaviours that could be analysed in response to pathogen sensory cues. Finally, these tools/approaches could be applied to wildlife management and conservation (Tuia et al., 2022) by investigating, for instance, animal movements after a disgust-based intervention.

4 | DISGUST RECIPES: FROM SOLITARY TO COLONIAL SPECIES

Below, we provide a basis for testing disgust across landscapes, contexts and species, at different levels of sociality. According to the social system, ecology and resources on which each species subsists, we expect different trade-offs at play and thus different responses (see Table 1). The selected examples below (Figure 4) are highly relevant models to study disgust, disease avoidance and applications as they are representatives of given social and sensory environments, ecological niches, and life histories with their varying levels of pressure regarding disease, predation and competition.

4.1 | Relatively solitary species

Due to their low frequency of interactions with conspecifics, solitary species are less exposed to socially transmitted pathogens and endoparasites (except during reproduction). Disease risk, nonetheless, goes beyond conspecifics. Resources present in the habitat and proximity with other species also entail a risk of infection/intoxication and require investment in ART strategies. In fact, nearly 70% of mammals are solitary (Lukas & Clutton-Brock, 2013). The Javan slow loris *Nycticebus javanicus*, for instance, is a small arboreal, nocturnal and territorial primate from West Java, Indonesia, with the capacity to produce venom to compete with conspecifics (Nekaris et al., 2020). Little is known about its parasite and pathogen handling strategies. Given their lifestyle, it is possible that slow lorises did not evolve a similar sensitivity to soil- and faeces-contamination as (semi-)terrestrial and group-living primates did (see e.g. Poirotte et al., 2019; Sarabian & MacIntosh, 2015). Arboreal and group-living female woolly monkeys *Lagothrix lagotricha poeppigii* (Ll) and grey mouse lemurs avoid food contaminated by conspecifics (both) and their own faeces (Ll) to various degrees, but they do not avoid soil-contaminated food (Ll; Philippon et al., 2021; Poirotte & Kappeler, 2019). Slow lorises may be less careful about where they defecate compared to social arboreal primates who would, for example, select tree branches lower than foraging sites and having less foliage beneath to avoid faeces exposure among the group (Gilbert, 1997). Note that reinfection is probably less costly than novel parasite/pathogen acquisition, which may have alleviated certain pathogen selective pressure on solitary species/sexes and resulted in an absence of avoidance in the associated contexts (see e.g. Poirotte & Kappeler, 2019). One potential avenue to investigate pathogen avoidance in *N. javanicus* and related species would be to conduct foraging experiments with sensory cues simulating disease risk. Considering the ecology of the species, individuals may avoid consuming food and returning to sites associated with perceived disease risk, for example with faecal contamination from other arboreal non-predator species but not soil or conspecific faeces contamination.

Each habitat has its own specificities, which should be considered in disgust and disease avoidance. Parasites found on land and in water are different and well adapted to these environments. In aquatic environments, they do not desiccate, can survive longer outside their host and are more easily transported (McCallum et al., 2003; Poulin & Morand, 2004). Moreover, toxic biological contaminants such as heavy metals are largely found in aquatic ecosystems; suspended in water, deposited in sediments or accumulated in animals (Ding et al., 2022). These high concentrations of pollutants and high exposure to parasites mean that aquatic species should be especially prone to handle these risks. For example, cephalopods such as the common octopus *Octopus vulgaris* are susceptible to environmental and prey contamination by heavy metals and pharmaceuticals to which they may respond with avoidance after tasting the prey (see Altman, 1971 for laboratory experiments with a bitter-tasting chemical). Alternatively, cephalopods may accumulate heavy metals in their digestive gland and detoxify them (Penicaud et al., 2017; Rodrigo & Costa, 2017) by producing proteins that bind to metals to prevent oxidative stress (Sillero-Ríos et al., 2018). If doses are too high, Sykes et al. (2020) suggest that cephalopods

TABLE 1 Summary of the proposed disgust-related avoidance behaviour experiments across species and other proposed taxa. The experiment type is noted as "H", "T" and/or "F" for habitat, tool and food selection, respectively. The potential trade-offs with avoidance are indicated as per previous studies and contexts. Similarly, the main strategy predicted to be used to handle the disease threat ("disgust elicitor") is annotated (A for *avoidance*, R for *removal*, T for *tolerance*). The common thread across experiments is their binary dimension (disgust elicitor(s) vs. control).

Social system	Species/taxa	Lifespan	Habitat & activity	Experiment type	Disgust elicitor	Potential trade-off with avoidance	Predicted ART investment
Relatively solitary	Common octopus Other octopods	Short	Aquatic Diurnal/ Nocturnal	H, T, F	Pollutant	Protection against predators and energy intake	R
	Javan slow loris Other lorises, tarsiers, lemurs	Short	Arboreal Nocturnal	F, H	Faeces, soil	Previous captivity	A, T
Group-living	Carrion crow Other crows, pigeons, *cockatoos	Short *Long	Arboreal Diurnal	F	Drug (e.g. carbachol)	Energy intake	A
	Asian elephant Other ungulates (wild pigs, deers)	Long	Terrestrial Diurnal	H	Pathogen-related odour	Energy intake	A
	Human Other types of wildlife tourists (e.g. for other great apes)	Long	Terrestrial Diurnal	H	Carcass, selfie images	Ego satisfaction (social media presence)	A
	Red-eared slider Other sliders	Relatively long	Semi-aquatic Diurnal	H	Faeces	Physiological needs	T
Colonial	Adélie penguin Other seabirds (penguins, albatrosses, puffins)	Relatively long	Semi-aquatic Diurnal	H	Faeces	Breeding success	T

FIGURE 4 Proposed species and ecological contexts for disgust-related avoidance behaviour experiments and their applications: (a) common octopus in a shallow coastal water; (b) Javan slow loris in a highly degraded habitat; (c) red-eared sliders at a basking site; (D) Asian elephant around crop plantations; (e) carrion crow in an urban environment; (f) tourist visiting mountain gorillas; (g) Adélie penguins at the colony's nesting site. Photo credits (from a to g): Eduardo Sampaio/Captain Darwin; Andrew Walmsley; Cécile Sarabian; Comparative Cognition for Conservation Lab, Hunter College, CUNY; Kenneth Keuk; Ryoma Otsuka; Andrew J. J. MacIntosh.

such as octopuses may have the ability to vomit and expel these contaminants. The common octopus can serve as a model to test how aquatic and relatively solitary species, relying on safe shelters for reproduction and survival, cope with biological contamination in their natural environment. One could manipulate dens, tools (i.e. bivalve shells or stones to block dens and hide from predators; Mather, 1994; Figure 4a) and prey by coating them with a pollutant to create an 'aquatic landscape of disgust' and test for consistency in avoidance across time and contexts among individuals.

4.2 | Group-living species

Proximity and habitat sharing with conspecifics or closely related species favour faecal-oral parasite transmission via contaminated substrates, food and water, but also airborne pathogen transmission via droplets and contaminated environments. Therefore, group-living species may be exposed to a higher diversity of parasites and pathogens than relatively solitary ones. Social species are expected to have developed an arsenal of pathogen handling strategies, relative to other factors that may increase or decrease their susceptibility to disease, that is ecological niche and life history parameters (Lopes et al., 2022). For instance, elephants, given their fission-fusion social system and herd size (up to 100 individuals in African savannah elephants *Loxodonta africana*), diet, habitat, and long lifespan are under high endoparasite/pathogen pressure (Coulson et al., 2018; Jiang et al., 2020; Lynsdale et al., 2017; Patterson & Ruckstuhl, 2013). What we know regarding parasite handling strategies in these megaherbivores is yet limited to a few behavioural studies. In the arid regions of southern Africa, elephants avoid artificial waterholes with high levels of *Escherichia coli* contamination (Ndlovu et al., 2018) and dig wells with their feet and trunks to potentially reduce the acquisition of such faecal coliform bacteria (Ramey et al., 2013). A recent experiment also shows that they would avoid crossing a line to get food behind it when that pipe/string is impregnated with volatile compounds present in carnivore faeces (indole or phenol; Valenta et al., 2021). The latter are released during the decomposition of proteins by pathogenic bacteria elephants are susceptible to be infected with. Further tests are now needed to discriminate perceived predation from perceived disease risk here. Elephants *Elephas maximus* may also tolerate gastrointestinal nematode infection within the group, as if the benefits of sociality outweigh the costs of parasite infection (Lynsdale et al., 2022). Much more remains to be tested when it comes to disgust and disease avoidance, such as whether pathogen-related smells drive their foraging decisions and space use at a landscape level.

4.3 | Colonial species

Colonial species can live in groups of dozens to millions of individuals in close association to procure strong mutual benefits such as stronger defence against predators, resistance against disease or thermoregulation (Le Bohec et al., 2005; Traniello et al., 2002), traded-off with increased pathogen transmission risk. Social insects, bats, mandrills or banded mongooses are good examples of these.

In these species, avoidance of sick conspecifics is not always observed (Poirotte & Charpentier, 2020; Stockmaier et al., 2020). In fact, resistance or tolerance might even be more efficient (Fairbanks et al., 2015; Traniello et al., 2002). Colonies can gain collective immunity by aggregating and using a dilution effect. Rabbits *Oryctolagus cuniculus*, for instance, do not avoid each other when outbreaks of viral haemorrhagic disease occur, but instead increase density in burrows, increasing the rate of contacts and thus quickly gaining immunity to the disease before it becomes highly infective and transmitted by fleas (Calvete et al., 2002). In other colonial species such as those living in rapidly changing cold habitats, little is known about disease handling strategies. Adélie penguins *Pygoscelis adeliae*, for instance, can be infected by various protozoa (e.g. *Cryptosporidium* spp., coccidia; Barbosa & Palacios, 2009), pathogenic bacteria and viruses (poliomaviruses; Varsani et al., 2015), which are passed on via contact with faecally-contaminated substrates during preening, feeding or stone gathering for nest building. During the breeding season on shore, male Adélies arrive first to build the nest while females arrive later to choose their nest and partner (Black, 2016). Individuals are particularly at risk of infection with direct life cycle pathogens due to the nests' proximity with each other and penguins' behavioural tendency to propel faeces at the edge of their nest (Meyer-Rochow & Gal, 2003). Future studies should investigate nesting location strategies and potential trade-offs with parasite infection, predation risk and mating/nesting success, as nests located in the centre may be more at risk of infection while nests at the periphery, more at risk of predation (see Schmidt et al., 2021) and more selected by young penguins (Penney, 1968).

Sociality, habitat, but also lifespan and activity should be considered as factors influencing disease risk and, thus, the investment of species in protective and defensive mechanisms against pathogens. Long-lived species, for instance, may not be able to afford contacting pathogens with a high cost given their slow developmental periods and late reproductive success. They may therefore have evolved specific disease risk recognition mechanisms linked to their sociality and ecology and invest more in avoidance than in other strategies (i.e. R, T; Figure 1). On the other hand, short-lived species may rather invest in disease resistance or have evolved other features (e.g. solitary lifestyle, arboreality) limiting their exposure to certain pathogens. Investigating the interactions between the sociality, life history and ecology of species and their investment in behavioural immunity versus defence against predators and competitors would be a fascinating avenue for future research.

5 | APPLICATIONS OF DISGUST TO WILDLIFE MANAGEMENT AND CONSERVATION

Disgust-related avoidance behaviours can apply to a variety of problems faced by different species and populations (see Table S2). Below are some examples applied to key areas of concern: conservation, human-wildlife interactions and environmental change.

5.1 | Endangered species survival: Rehabilitated primates in fragmented landscapes

Habitat loss and the wildlife trade are among the main threats to primates (Estrada et al., 2017). Seizures, trafficking and finds by local people due to habitat fragmentation all result in arrivals at sanctuaries. These organizations host and may rehabilitate primates into their natural environments. Critically endangered Javan slow lorises, for example, are rehabilitated in nearby lowland fragmented forests, but show low survival rates (for this and other closely related species; Kenyon et al., 2014; Moore et al., 2014). Moreover, habitat fragmentation may increase ground use by slow lorises, as a result of connectivity loss, making them vulnerable to different parasites and predators while moving from tree to tree (Rode-Margono et al., 2014). Previous research in woolly monkeys shows a correlation between time spent in the pet trade/captivity and reduced parasite avoidance behaviours (Philippon et al., 2021). Based on Philippon et al.'s (2021) findings, we predict that individuals with longer times spent in captivity (i.e. pet trade and sanctuary) would express lower pathogen risk sensitivity compared to individuals released soon after capture; and that individuals with higher pathogen risk sensitivity would show higher survival rates post-reintroduction. Such information is crucial to design effective tests at sanctuaries, reduce time spent in captivity before release, and inform individual release decisions along with other parameters (e.g. age, body condition, etc.) to improve rehabilitation success.

5.2 | Invasive species and disease risk mitigation

Invasive species are one of the main drivers of biodiversity loss (Butchart et al., 2010). Conditioned aversion learning could be used to limit the establishment or the spread of non-native species. For example, red-eared sliders *Trachemys scripta elegans* compete with native turtle species for food and basking spots (Cadi & Joly, 2003; Polo-Cavia et al., 2010). Sliders *Trachemys* spp. are the most traded turtles in the world (Herrel & van der Meijden, 2014), despite import now being banned in many countries (Kitowski & Pachol, 2009). When turtles grow larger and captive care becomes more difficult, pet owners often release them into nature. They are considered invasive in most of their introduced range (Lowe et al., 2000) and can be detrimental to native turtle species by competing for food and basking spots (Cadi & Joly, 2003; Polo-Cavia et al., 2010). Reasons for their success include their relatively rapid reproductive rate, adaptiveness to habitats and environments, flexibility of diet and resistance or tolerance to parasites (Deng et al., 2021; Zhang et al., 2020). As such, it is essential to reduce their interaction with native species and their use of key habitats for those species. CTA can be used to train sliders to avoid certain foods and possibly species. By associating a specific food with a negative outcome (feeling sick), the animals will rapidly learn to avoid these food types, leaving them available for native species. This would have to be done extremely carefully to ensure native species are not exposed to the same conditioning.

However, it may be possible to do this by exposing animals at times of year when sliders are active while native species are not, or, by selecting areas where native species have already been lost. Specific food avoidance by sliders would give the habitat a chance to regenerate to allow reintroduction of native species.

5.3 | Crop-foraging and use of agricultural lands

Human-wildlife interactions related to agriculture are ubiquitous and can be deleterious. Human-elephant conflict around agricultural fields, for example, causes many human and elephant deaths every year (Naha et al., 2019; Shaffer et al., 2019; Thirgood et al., 2005). The animals' motivation to forage on crops and to take risks entering human landscapes is likely related to nutritional/mineral needs (African and Asian elephants: Branco et al., 2019; Rode et al., 2006; Vogel et al., 2019; chacma baboons *Papio ursinus*: Findlay & Hill, 2020; Walton et al., 2021) and/or food availability (wild boars *Sus scrofa*: Ballari & Barrios-García, 2014; Herrero et al., 2006). Few of the crop deterrent methods (e.g. fencing, devices using sounds and/or lights, chemicals) consider the animals' behaviour (Mumby & Plotnik, 2018; Shaffer et al., 2019). These methods are mainly short-term solutions for recurrent interactions that fail to account for the animals' decision-making or their complex energy needs. In contrast, we propose a system that does not physically exclude wildlife from a landscape but instead encourages it to avoid certain locations (entering crop fields) by increasing perception of certain risks (e.g. disease).

5.4 | Urban pests

Conditioned-taste/food aversion could reduce animal scavenging behaviour on garbage and potentially apply to other human-wildlife negative interaction contexts. General urban nuisance, foraging on anthropogenic resources and human health and safety are also reported to create conflicts (e.g. crows *Corvus* spp: Japan Ministry of the Environment, 2018; bears *Ursus americanus*: Lewis et al., 2015; wild boars: Fernández-Aguilar et al., 2018; Jansen et al., 2007). Current mitigation methods are not always legal and ethical (e.g. poisoning or culling; Chapron & Treves, 2016; Di Blasio et al., 2020) nor again consider the animals' adaptive behaviours (e.g. yellow trash bags that crows cannot see through). Inducing aversion through taste, smell, vision and social spread (even in relatively solitary species, see e.g. Mazur & Seher, 2008) could have short term costs but longer-term benefits in species with such relevant sensory modalities.

5.5 | Ecotourism and pathogen exchange prevention

Disease risk is an inherent component of great ape ecotourism (see Glasser et al., 2021; Molyneaux et al., 2021), which may be traded off against knowledge and awareness about infectious disease transmission as well as with the demand by tourists for proximity. In response to the COVID-19 pandemic and its potential severe outcomes on great ape populations (Kalema-Zikusoka et al., 2021; Melin et al., 2020), online and onsite education materials were developed (see www.protectgreatapesfromdisease.com and www.gorillafriendly.org/pledge/). These campaigns emphasize disease risk and could be a starting point into testing how visual cues of disease, pathogen disgust sensitivity and visitor behaviour may interplay. Further initiatives based on the adaptive system of disgust could use tools and behaviours associated with great ape tourism (i.e. smartphones and selfies) to develop a mobile application promoting social distancing and mask wearing (see www.conservationx.com/project/id/1544/wildpic). Otsuka and Yamakoshi (2020) showed the importance of the social media interface in gorilla *Gorilla beringei beringei* ecotourism and how video views and likes are correlated with the simultaneous exhibition of humans and gorillas in preview images of videos. Successful strategies to keep distance between tourists and gorillas would also reduce gorilla overhabituation, which can have cascading effects in other contexts (besides tourism) of human-gorilla interactions, such as crop foraging (Humle & Hill, 2016). Note that human-wildlife negative interactions are often seen from the human perspective but the drawback effects on gorillas' health should not be neglected (Hanes et al., 2018; Kalema-Zikusoka et al., 2021; Whittier et al., 2021).

5.6 | Sea water pollution and climate change

As sea water pollution and climate change outcomes are worsening (Landrigan et al., 2020), disgust could have further applications for species living in habitats at the forefront of such issues. The study of disgust in the common octopus could shed light on how cephalopods cope with prey and habitat contamination, and to what extent. On the other hand, Adélie penguins may face climate change differently depending on their location (asymmetry between West and East Antarctica) and latitude, with populations decreasing or increasing following sea ice fluctuations (LaRue et al., 2013). This can have cascading effects on pathogen spread and may help to predict different scenarios (both short-term and longer-term). Future studies should consider how sensitivity to pathogen risk varies across colonies affected differently by climate change.

We do not claim to have new miracle solutions for all the above. We rather propose to explore behaviours that have not been much considered in certain taxa/species and use such information to design evolutionary-based conservation strategies.

6 | CONSIDERATIONS AND PERSPECTIVES

According to the 'sociality-health-fitness nexus', the sociality and ecology of a species predict its predisposition to infection with certain types of pathogens (Kappeler et al., 2015). Solitary species may be less susceptible to directly transmitted pathogens while social species may be more vulnerable to them (Figure 5). On the other hand, solitary species should be more threatened by predation and conspecific competition, against which they may have evolved other defence strategies (e.g. slow loris; Nekaris et al., 2020), while social species may gain protection from the group (e.g. Asian elephants) or use collective strategies to defend themselves against predators (e.g. Adélie penguins; Ainley et al., 2005). Further research on the ecology of disgust should consider both perceived disease and predation risks ('ecology of peril'; Doherty & Ruehle, 2020; Moleón & Sánchez-Zapata, 2021; Figure 5), or to go even further, consider disease, predation and competition risks. These risks are interconnected, although the pressure of one may vary according to the ecology of a species. A landscape of risk (considering the three types of risk) could also be used in the design of effective human-wildlife conflict mitigation strategies while adapting to ecological fluctuations and individual variability.

Testing responsivity to pathogen risk under natural conditions might be challenging from several perspectives. In cases of practical challenges (e.g. due to the terrain), either long hours of observations and/or novel technologies are required, by focusing on, for example 'microbehaviours' (behaviours at a refined scale) associated with disease risk (what/whom do the individuals contact, eat, etc.), or complementary experimental tests in captivity. In some cases, it might also be difficult to obtain approval from ethical committees and conduct research in protected areas (e.g. tourists, penguins). This may be because of the required environmental/food contamination or because experiments touch upon lucrative businesses. Associating disgust to the latter may be perceived in a negative way. However, in the current context of climate change and pandemic, the outcomes of such research should be perceived as bringing more benefits and knowledge than drawbacks.

As one should carefully consider the ethical, moral and political implications of using disgust in public health campaigns (Lupton, 2015), the same dimensions should not be neglected in fundamental or applied research with animals. In an example of an experiment with gorilla tourists, the side of the gorilla can be taken by presenting non-photoshopped images of the outcomes of respiratory diseases in an endangered species. The idea is not to shock viewers but to make them associate their behaviour with an outcome, which can be negative, by visualizing it and calling on their adaptive system of disgust.

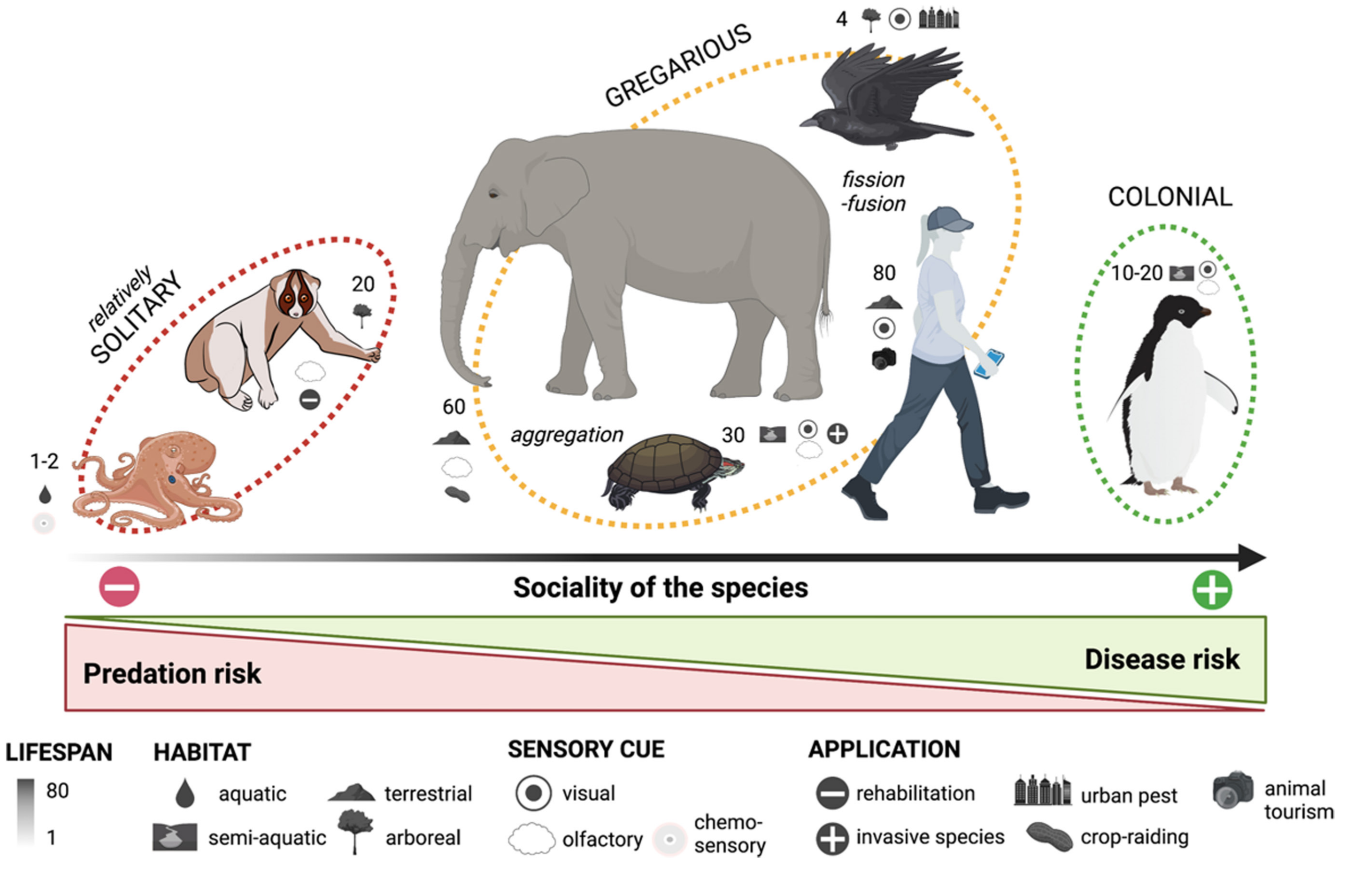

FIGURE 5 Sociality and peril. Disease and predation risks are predicted to vary with the sociality of the species; the former increasing with social traits (aggregation: red-eared slider; fission-fusion: Asian elephant, carrion crow, human; colony: Adélie penguin) while the latter increases in relatively solitary species (e.g. common octopus and Javan slow loris—credit: Kenneth Keuk). Model species vary in their lifespan and habitat, which may affect their investment in avoidance/defence strategies against parasites/pathogens and predators. The main sensory cue that can be used in future experiments (adapted to the ecology of the species) as well as wildlife management and conservation applications are also represented. Created with BioRender.

Future experiments could compare whether taking the side of gorillas is leading to more distance and mask wearing than when disease risk is emphasized for humans. For other species (e.g. octopus, loris, slider, crow), we propose experiments with biological contaminants that are already present in the species' environment or with substances that induce short-term sickness (Tobajas et al., 2019). Both strategies are based on unpleasantness or a certain degree of illness, which confers on them their evolutionary relevance and effectiveness. The proposed experiments are not supposed to create habituation to the presented cues, except for the mild ones depending on the implied trade-offs. Researchers should ensure that non-target species have no or limited access to anything presented during experimentation (Smith et al., 2022), which may have unwanted cascading effects, and the design should be as specific as possible to the diet and ecology of the species (e.g. drilled gum discs for slow lorises).

Finally, we propose to create a database (e.g. "ManyPTA"—Parasites To Avoid), which would gather the existing literature (Table S1) but also the pending experiments and the animal taxa from which we know very little (e.g. crocodilians, chameleons), where scientists and practitioners can communicate about what works and what does not. For the applied side, a collaborative platform that exchanges knowledge, ideas and experiences about human-wildlife interaction issues such as 'ENCOSH' (see www.encosh.org) could be the place to propose a 'disgust toolbox' for wildlife management and conservation.

AUTHOR CONTRIBUTIONS

Cécile Sarabian conceived the novel conceptual and application ideas, designed the experimental frameworks with inputs from all co-authors and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No data were used in this review.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Summary of parasite/pathogen avoidance strategies in wild animals.

Table S2. Species/taxa examples for the applications of disgust to wildlife management and conservation.

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