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Don’t! The science behind revulsion

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Chapter 2. Into the Hot Zone

> “May I never lose you, oh, my generous host, oh, my universe. Just as the air you breathe, and the light you enjoy are for you, so you are for me“
>
> –Primo Levi, Man’s Friend

To make an animal it takes proteins, fats, starches, fluids and micronutrients. These ingredients combine to make a tempting calorie- and nutrient-rich dish for other animals to feast on. We are all familiar with the food web: larger, stronger, faster predators eat smaller, weaker predators, which eat smaller, weaker ones, and so on down to the herbivores grazing on the autotrophic plants, bacteria or algae that fuel the whole system.

But there is more than one way to make a meal of another animal. Rather than investing lots of energy in the hunt and chase, some animals have evolved a less dramatic strategy – parasitism. These animals climb on board, worm their way in and stow away. They then have a smorgasbord of tissues and bodily fluids, not to mention shelter, transport and mating opportunities.

The parasitic way of life is pretty good and explains why parasites outnumber predators on the planet, both in terms of number of species, and in total biomass[i]. Imagine, for a moment, one of those BBC wildlife series where we see life at night through an infrared lens. The shapes of warm animal bodies show up bright red against their cool nocturnal environment. Pink birds fly through a dark purple sky. Lizards glow yellow or orange. David Attenborough breathes to camera: "…and look at the glowing patch left in the nest as the owl takes off on her nightly hunt!" Now, instead of looking at the world through a heat-detecting lens, switch to a parasite-detecting lens. What does the world look like? In fact it looks much the same, but where once stood the birds and the lizards are silhouettes of parasites. The animal bodies are bright red.

Parasites are everywhere, infesting skin, tissues and guts; even the follicles of your eyelashes teem with microscopic worms. Every free-living animal is a seething mass of parasites. Our parasite-detecting lens reveals, not just the fleas, lice and ticks hiding in the pelt of the animal we are filming, it also shows the worms in its gut, the microbes in its flesh and the millions of viruses that infest its every cell. Seen through this lens, all animals light up bright red – they are hot zones full of parasites.

Yet, all animals do a good job of staying whole, of keeping their delicious bodies to themselves, of staying alive, with their parasites under control, at least for long enough to procreate. No one has yet been able to build a detection system that can scan for tiny bugs and invisibly small microbes hiding inside living organisms. But animals do have systems for detecting and avoiding parasites. And these parasite radars must be trained on particular parasites, those that are particularly risky to those particular animals. Mice have to avoid mouse nematodes, not fish nematodes.

Rhinos have to avoid rhino viruses and not human influenza viruses. Every animal has to be able to detect the types of parasite that are specific to its kind. So a well-designed animal should have a parasite-detection system that is capable of detecting not just any parasite hotspot, but those that contain the most threatening varieties of parasite.

But if parasites can't be seen and they don't give off any radiation that can be detected on film, what's an animal to do? So if, for example, a lobster meets another lobster giving off an odd odour, then maybe it shouldn't share a den with it, as it might be infected with a lethal virus. Or if a killifish encounters another killifish with black lumps all over its body then perhaps it should find another shoalmate. If a salamander is hungry perhaps it shouldn't risk dining on another salamander of the same species, as it might ingest pathogens infectious to salamanders. And a reindeer should probably migrate regularly so as to avoid eating grass contaminated with parasites cysts from the droppings of other reindeer.

All of the animals that are alive today have ancestors that were good at parasite detection and avoidance. Those that didn't have those abilities simply got eaten up by bugs, and so ended their genetic history. Animals filter incoming sensory information – sight, smell, taste, touch – use it to compute likely parasite risk, and then respond to that risk, just as if they really did come equipped with parasite-detecting lenses. This skill seems to be found in all animals, humans included. And we humans have given parasite-detecting devices a special name: 'disgust'. Though we may have invested it with special significance and a special name, the human parasite-detection and avoidance system doesn't differ much from that of other animals, and surely it must have a common ancestry[ii]. We humans have a few unusual abilities, built on top of our animal abilities; like our capacity to imagine parasites, and to learn from what we imagine, and our skill in the use of microscopes (real parasite- detecting lenses). But for the most part, we behave as most animals do. So if we want to understand human disgust-related behaviour we should turn to other animals.

Animals have four different ways of avoiding paying the dire fitness costs of being invaded by body-snatchers. First, they can avoid close contact with animals of their own species, especially when they are sick, because this is where the best adapted and most infectious parasites are likely to lurk. Second, they can avoid other species of animal which might be vectoring parasites that can jump from species to species. Third, they should stay away from places and things that might be contaminated with parasites or their progeny. And finally, particularly enterprising animals can alter the world they live in, in such a way as to make it inhospitable to parasites[iii].

Task 1. Avoid others, especially if they are sick

Whilst there are various reasons why animals of the same species might cuddle up to one another, viewed through parasite-detecting lenses, intimacy is far from a great idea. Female housemice (*Mus musculus*), for example, take a good sniff of prospective mates, and if they detect a whiff of the protozoan worm-like parasite *Eimeria vermiformis,* then they move on to the next male[iv]. In one famous experiment, researchers painted red lumps on the wattles of the males of half of a flock of Sage grouse (*Centrocercus urophasianus)* to mimic the effect of an ectoparasite infestation. These apparently lousy males had far less mating success than those which had not been so adorned[v].

Choosing a healthy-looking bird as a mate has two advantages, it helps get good genes into your offspring and it also prevents you from catching something nasty, like a louse carrying a virus, in the here and now. An unhealthy partner could make you sterile or, worse yet, can introduce congenital disease into your breeding line. Disease avoidance offers a good additional evolutionary explanation for why birds prefer healthy-looking birds[vi].

Another way that animals test the health of a prospective mate is to provoke them to fight each other and see who comes out on top. When female squirrels and possums display their sexual availability prior to oestrus, it provokes competition between males. The winner of the battle, who is likely to be the healthiest and least parasite-ridden, gets the girl[vii]. Humans may not have a penis bone for similar reasons. Having a big showy erection is a great way of displaying to a prospective mate that you don't have any fulminating diseases that could interfere with all those delicate hydraulics[viii].

In general its advantageous to avoid sick individuals of the same species. About 7% of bullfrog *(Rana catesbeiana)* tadpoles have a yeast infection which reduces their mobility and may lead to death. Given the choice, healthy tadpoles avoid going anywhere near those that have the infection[ix]. Similarly, when experimenters injected Killifish (*Fundulus diaphonous*) with black inkspots to mimic the effects of a common parasite, other killifish preferred not to shoal with them[x]. Caribbean spiny lobsters (*Panulirus argus),* oddly enough, quite social creatures, refuse to share dens with lobsters infected with the PaV1 virus[xi].

Parasite-detecting lenses are particularly helpful if you are a social species. Whilst being social has its advantages – such as safety in numbers and the benefits of cooperation – it has a big downside in the form of greater risk of disease. Social primates are careful who they accept into the troupe; they will generally only welcome a new member after a long period of quarantine. During that time the troupe will often attack the outsider, testing its state of health. Any overt signs of sickness decrease the chances of acceptance.

Parasite pressure may actually place a limit on group size – in habitats rich in pathogens, such as the warm, humid rainforest, typical troupe size for colobus monkeys is about nine, whilst in the hot dry savannah of highland Ethiopia, with much lower pathogen loads, gelada *(Theropithecus gelada)* group size can run to several hundred[xii]. Through parasite-detecting lenses members of foreign troupes appear as parasite hot zones – especially because they might be carrying new pathogen variants, ones that the home group have no immunity to. This may be why primates are careful to limit contact with foreign groups, communicating only at a distance by calling, and by giving way to each other when they cross in the forest. Instinctive xenophobia may be a useful adaptation for a social species.

Another good way of not catching a parasite is to avoid meat, especially that from the same species. Ecologists have puzzled over why cannibalism is so rare, observing that very few species satisfy their nutritional needs by nibbling on their neighbours. Parasites offer an explanation: one's cousin is a hot zone. A relative is more likely to carry an infection infectious to oneself than is a more distant species. The larvae of Tiger Salamanders (*Ambystoma tigrinum*), for example, have cannibal and non-cannibal varieties, but the cannibals tend to carry much higher numbers of intestinal nematodes and bacteria than their non-cannibal cousins[xiii].

Human also, are adept at avoiding catching diseases from others of the same species. We turn cannibal only in extreme circumstances, we sit as far as possible away from others at table or on trains, and if someone shows any visible signs of disease we tend to avoid contact and terminate interaction early[xiv]. Three of the six categories of human disgust response that our study identified concern others of the same species - people who look sick, abnormal or disfigured, people as sex partners, and people who display poor hygiene[xv].

Task 2: Stay away from other species, especially parasites, parasite hosts and vectors

Apart from their own kind, what further parasite hot spots might well-adapted animals avoid? Other animals that are also parasites themselves, that host pathogens, and those that are used by pathogens as vectors all pose threats. Animals have evolved amazing repertoires of self-defence behaviour, from the smallest worm to the largest mammal.

Take *C. elegans*, for example. This tiny nematode worm, with only 302 neurons to his name, is much beloved by biologists as a model system for understanding animal physiology and behaviour. This 1mm long creature is clever enough to detect when there is a parasitic bacterium in its petri-dish and turn around and flee from it, in seconds (see the film on book website). However, when it is offered non-parasitic bacteria to eat, it worms quickly over to gobble it up[xvi]. Ants are similarly discriminating; feeding on the corpses of other species, but scorning those infested with parasites[xvii]. Fish are known to avoid disease vectors; the Rainbow Trout (*Oncorhynchus mykiss)* can detect and swim away from parasitic eye flukes that cause blindness, and, as a result, suffer fewer infections[xviii].

The surface of an animal is like a tablecloth spread for a picnic, inviting hordes of hungry parasites to a free meal, (not to mention other freebies such as shelter, mating opportunities and a ride to a new host, when the first has been exhausted). Multiple species of lice, fleas, ticks, mites, blood-sucking flies, mosquitoes, leeches, as well as bacteria and fungi exploit or colonise the epidermis of every species of vertebrate. And vertebrates invest a lot of effort to get rid of them. Cattle stamp their feet and swung their heads in response to biting tsetse flies, fish scrape themselves on rocks and vegetation, as do elephants. Vampire bats (*Desmodus rotundus*) scratch to remove batflies[xix], while birds preen and impala (*Aepyceros melampus*) use their teeth as tick combs.

Over 250 species of bird are known to 'ant'; rubbing crushed insects such as ants or millipedes over their plumage. This distributes compounds that protect them from bacteria, fungi and arthropods[xx]. Grey squirrels and Colobus, Owl and Capuchin monkeys also rub their fur with leaves and fruit juices, probably for similar reasons[xxi]. When an experimenter stopped up the gaps in an impala's teeth on one side only, the side of the body that thus couldn't be groomed rapidly became tick-infested[xxii]. And the effects of ectoparasite infestation can be serious: a calf with a moderate tick load, for example, gains 10–44 kg less per year than a tick-free calf[xxiii]. Blood-sucking mites significantly reduce the body mass of house sparrow (*Passer domesticus)* chicks[xxiv]. Apart from absorbing nutrients directly, biting insects serve as disease vectors; they introduce other, smaller, epiparasites such as the mosquito-borne plasmodium which causes malaria in perching birds and the tick-borne flavivirus which causes encephalitis in cattle. Parasites within parasites are a double burden, best avoided by all behavioural means possible.

Among primates grooming to remove ectoparasites is of so much value that it can be exchanged for other resources like food or sex. Long-tailed Macaques (*Macaca fascicularis)* have a biological market system where they pay for sex at the going rate in the currency of time spent grooming.[xxv] And what better time for a parasite to hop onto a new host that when the hosts are having sex? Ectoparasite transmission during mating has been documented in guppy, stickleback, sage grouse, pheasant, rock dove, barn swallow, grackle, zebra finch, and bower bird[xxvi], not to mention humans.

Most animals need sex to produce offspring, and can't avoid the disease risk that this brings. But they can take precautions. Primatologist Sean O' Hara observed that chimpanzees (*Pan troglodytes*) in the Budungo forest in Uganda regularly cleaned their penises, either with leaves or with their hands, after copulation[xxvii]. And rats that are prevented from grooming themselves after sex catch more genital infections[xxviii].

Biologist Mark Pagel has proposed that being covered in a furry blanket, which requires constant grooming to keep lice, ticks and other parasites under control, was so costly for some primates that, once they found other ways of keeping warm (fire, caves or clothes, for example), they pretty much gave up on hair altogether[xxix].

In a hot zone world, animals also face a real dilemma when it comes to deciding about food. On the one hand a morsel may be tasty and nutritious, but on the other hand, it may contain a hungry microparasite. This is one of the most ancient problems animals have had to solve, and, as with sex, each species has had to find a balance; a trade-off between the likely benefits and risks. To the oystercatcher *(Haematopus ostralegus)* the biggest cockles *(Cerastoderma edule)* are the most appetizing and easiest meal. However, the biggest cockles also harbour the most helminth parasites, for which the birds are the definitive hosts. Ecologist Ken Norris showed that birds were feeding not on the smallest, least-parasitized cockles, because they were too much effort to open, nor on the fattest, but the middle-sized cockles, balancing the need for a cheap and a safe feed[xxx]. Butterfly fish (*Chaetodon multicinctus*), on the other hand, strike a different balance, actually preferring to feed on the bulbous lumps produced by coral infected with the cercariae of a tiny trematode. It seems that the extra energy gained from eating these fleshy extrusions that can't retract themselves like healthy coral outweighs the costs of ingesting more parasites[xxxi].

Predators have the same dilemma. It is much easier to kill and eat the sicker, weaker members of a prey troupe, but the predator that does so runs the risk of ingesting the parasite that made that individual sick and weak. Prey killed by predators are consistently infected with more trematodes, nematodes, and ectoparasites than randomly collected individuals[xxxii]. Feasting on the sick and the dead requires investment in a really robust immune system.

Humans, of course, also need to perform task 2. One of the categories of human disgust that we identified is other species that might pose a parasite risk. We are repulsed by parasites themselves, when we can see them (or watch fictional versions in sci-fi horror movies), we avoid parasite hosts such as rats, and parasite vectors such as cockroaches. And we are extremely careful about what we eat, especially when the food is another species, or unfamiliar, or if it has been in contact with parasites.

Task 3: Stay away from parasite hot zones in the environment

Conspecifics and other species are not the only places to encounter parasites. There are some places in the environment that are hot zones and animals that can detect and avoid them have a comparative advantage in the race to get genes into the next generation.

Ants of the species *Temnothorax albipennis* avoid building nests in sites where they find dead ants because corpses signal a possible hot zone[xxxiii]. If *Acromyrmex striatus* ants encounter a patch of fungal spores close to their nest they close off the nearest entrance to help stop their nestmates from importing contamination[xxxiv]. The water flea, (*Daphnia magna),* has to make a difficult and dangerous trade-off calculation; if it swims near the surface it may be eaten by murderous predatory fish. If it swims near the bottom it may encounter the spores of murderous bacteria lurking in the mud. In a neat experiment Daphnia were forced to swim nearer to the bottom of their tank by the addition of 'extract of predator' to the top. They paid the price; picking up an increased load of microbial parasites[xxxv].

Using a nest is a handy adaptation for many species, providing shelter and protection from predators but the downside is that your nice cosy home can also become a hot zone for parasites. Biologists in Switzerland offered great tits (*Parus major*) two kinds of used nest boxes to choose from. One half were infested with blood-sucking hen fleas (*Ceratophyllus gallinae*), whilst the other half had been microwaved. Of the 23 pairs of great tits that started breeding, three quarters chose the parasite-free nests. The few that chose parasitized nests started their clutch an average of 11 days later, perhaps in the hope of out-waiting the fleas' breeding cycle[xxxvi].

Nests can also harbour larger parasites – other birds. Cowbird chicks throw out resident chicks from a nest and assume their place; at least 37 species of bird have been documented abandoning nests because of infestation with cowbirds[xxxvii].

Environments that are contaminated with excreta are also likely parasite hot zones. Soils that have been fertilized with dung produce richer, lusher more nutritious grass, but they also tend to contain more parasite larvae. Through parasite-detecting lenses the greenest grass shines brightest. In tests, sheep avoided grass laced with gastro-intestinal nematode-containing faeces. However, they became less picky about what they ate when they were hungry[xxxviii]; a phenomenon that has also been observed in humans. The parasitic potential of poo has even been evoked as an explanation for the phenomenon of animal migration. Reindeer and caribou may seek new pastures every year, not because of some mysterious wanderlust, but because they are looking for clean, dung-free pastures on which to feed, calve and rear up their young[xxxix]. When I alluded to this explanation for migration at a dinner given by anthropologists, one woman told me that she'd heard nomadic bushmen in the Kalahari discussing the same issue. "Its getting dirty round here, time to move on!" she heard one say to another. Another anthropologist related that Mongolian pastoralists do the same; timing migration to the build up of human waste in camp.

Human have one more, possibly unique (mice are another candidate[xl]), means of detecting possible parasites in the environment. Humans pay attention when a parasite hot zone comes into contact with another object and remember what has happened. Like the bird in the infrared camera that leaves a hot spot behind when it takes off, so humans remember the chain of contamination as if it were a series of hotspots, for example, avoiding food that has fallen on the floor, or a toothbrush that has been used by a stranger (labelled 'fomite' disgust in our web study).

Task 4: Modify the environment to discourage parasites.

There is one more strategy that animals can employ to reduce the dangers of parasitisation – rather than avoiding hot spots they can make sure that they don't arise. They can actively *modify* their environments so as to discourage parasites. An animal that has found a nice bit of habitat to feed and multiply in, doesn't want it to fill up with wastes. Faeces get in the way, contain toxins and harbour parasites and pathogens. So what to do with poo? As we've seen, you can just migrate and leave it all behind you. However, if you are a sedentary species, your ancestors will have evolved ways to deal with this problem.

Martha Weiss is the world expert on the poo-disposal practices of insects – although, entomologists call it 'frass', not 'poo'. She documents how leaf-cutting insects, like the caterpillars of the butterfly *Chrysoesthia sexgutella*, eat outwards from the centre of a leaf, leaving their droppings in the centre, whilst those that eat inwards, like the hispine beetle, leave a fringe of frass around the outside of the leaf. Her collection includes 'frass-flinging', 'turd-hurling' and 'butt-flicking'. Skippers use hydrostatic pressure to fling their pellets up to 38 times their body length away (153 cm for a 4-cm-long larva). Geometrid larvae hurl their turds with their thoracic legs, and noctuids jerk their abdomens to flick poo pellets more than 20 body lengths away. Butterfly larvae remove their frass by head-butting it away or by grabbing it with their mandibles to drop it off the leaf[xli].

Some animals are master compartmentalisers. Burrowing crickets use a specific corner of your chamber as a toilet, and clean it up later[xlii]. Spiders silk your turds into nest walls. Eastern tent moths (*Malacosoma americanum*) build silken latrines. They string huge webs across tree branches and use the lowest point as a toilet; when it becomes overloaded with faeces it detaches under its own weight and falls to the forest floor[xliii]. Faecal matter can also be put to good use. Some species of Ambrosia beetle larvae pierce the walls of their cradles to eject faeces, which the mother beetles carry off to manure fungus beds. Termites and some species of ants use their frass for nest building and for manuring their fungus gardens. Frass can even provide defense against predators. Cassidine beetle larva *(Coleoptera: Chrysomelidae*) attacked by predatory ants exude a huge sticky wet faecal shield over their anal forks (figure 1) which stops them from being bitten[xliv].

Figure 1 Faecal shield protecting the cassidine beetle larva from predatory ants. Pic Kenji Nishida

Though faecal wastes are a nuisance to solitary or familial insects, it is the social species that require sanitation systems. Ants and the other eusocial insects have to take parasite control very seriously because they are both sedentary, having to live with their wastes, and are highly related, making it easy for infections to spread. Most ants remove faecal material, as well as sick and dead colony members from their nests[xlv]. The social crickets (*Anurogryllus muticus*) share a special latrine chamber [xlvi] and social spider mites (*Schizotetranychus miscanthi*) always use the same spot within their nest for defaecation[xlvii].

Eusocial insects are masters at engineering their niches to make them unsuitable for pathogens and parasites. The nests of most social insects have many separate chambers rather than one huge hall. Mathematical models show that dividing nests into a series of rooms helps to slow epidemics of disease[xlviii]. Ventilation systems help to the same end. Wood ants *(Formica paralugubris*) build resin from pine trees into the fabric of their nests to inhibit the growth of bacteria and fungi[xlix].

Other animals keep their environs parasite free by not disposing of waste into them at all. Crab spiders (*Misumena vatia*) held in enclosed conditions refuse to defecate until they are released, at which point they head for the end of a leaf and dump over the side[l]. The larvae of bees, wasps and ants do not defecate at all; they hang on to their wastes in a 'blind gut' until pupation[li]. If workers then fail to clean it up, lethal fungi destroy the larvae[lii]. Overwintering Apis bees never defecate in their nests. Instead their rectums become distended with wastes, which are discharged on cleansing flights in the early spring. If half a colony of 40,000 bees sets off at the same time, defecating 20% of their body weight, the volume produced can be enormous. During the Vietnam War soldiers noticed a yellow rain which was thought to be a biological warfare agent, but it was probably the droppings of the giant honeybee (*Apis dorsata*) on its annual spring cleansing flight[liii]. In fact, bees are famously hygienic: not just defecating away from their nests, but also removing dead and diseased brood, and employing antibacterial compounds to keep their nests free of parasites[liv].

Apart from modifying their physical environment to avoid the evils of excreta, insects can also modify their social environments to get others to do their dirty work. Many species of ant have castes of cleaning workers who collect the faeces, the sick, the dying and the dead and carry them off to refuse piles a safe distance from the nest[lv]. There are subdivisions of labour, with the ants that do the dirtiest work – on the midden – being segregated from those that collect the wastes. Any attempt by midden workers to socialise with others is met with aggression[lvi]. Older workers with higher intrinsic mortality are more likely to do the dirty work[lvii]

Sedentary fish, reptiles, birds and mammals all have the same problems as insects – they need to engineer their environments to keep them from becoming parasite hot zones. They also build parasite-free homes, keep them clean, throw out wastes and get others to help in the task – if at all possible. Some fish species invest energy in not fouling their living and eating areas. In the Red Sea, the surgeonfish (*Ctenochaetus striatus*) stops feeding on the reef every five to ten minutes and swims to a spot of deeper water beyond the reef edge to defecate[lviii]. Captive pike *(Esox* *lucius)* defecate away from the 'home' area of their tank[lix] and Damselfish (*Plectroglyphldodon lacrymatus*) defecate in specific sites around the edges of their small territories [lx].

Defecating around the edge of one's territory is, however, not just a fish thing. It is common in many animals (for example, gecko, elk, orbi, and antelope), and is usually explained as scent marking[lxi]. However, it makes sense to keep parasite-ridden dung as far as possible from your feeding and living areas, as it does to deter rivals for your territory with the threat of the parasites that your dung may contain. Chimpanzees in zoos often throw faeces at passers-by, which may serve a similar function – to threaten rivals with parasites. Indeed several of our favourite swear-words are excreta-related. By throwing words such as *crap!*, *shit!* or *piss!* we metaphorically threaten our interlocutors with disease[lxii]. Washoe, the chimp that learntsign language, responded to scolding by calling her teacher a 'dirty toilet devil'[lxiii].

Parasites are a big problem for baby birds – nestlings are a juicy and defenseless feed for a variety of ectoparasites, including ticks, mites and blowflies. Parent birds try to make sure that the nest is not a hot zone for parasites by defaecating elsewhere, by removing nestling excrement, eggshells, foreign debris, ectoparasites and dead nestlings[lxiv].

Most birds keep their nests clean of droppings. The chinstrap and Adélie penguins are a spectacular example. Like the frass-flinging insects, they stand up on the edge of their stony nests, turn their backs nest-outward, bend forward, lift their tails, and shoot out a projectile poo. The expelled material hits the ground about half a metre away from the bird. Figure 2 is taken from a scientific paper calculating the hydrostatic pressures thus generated (which won an Ig Nobel prize for improbable research)[lxv]. In fact Emperor penguin (*Aptenodytes forsteri*) poo makes such a mess on the ice around nests that it can be seen from space, providing a useful means of monitoring the breeding success of this vulnerable species[lxvi]. Swallows (*Hirundo rustica*) do it differently. Parent birds remove the faecal sacs of their nestlings and fly away with them, as can be seen on youtube (youtube http://www.youtube.com/watch?v=Fa5CluKJxGM).

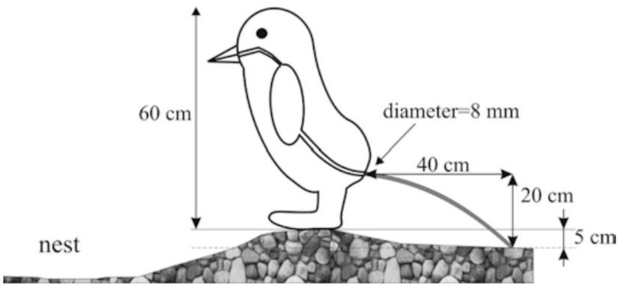

Fig. 1 Position of model penguin during defaecation and physical parameters used to calculate rectal pressure necessary to expel faecal material over a distance of 40 cm

Sometimes nests need more than just keeping clean, they need fumigating. Blue tits (*Parus caeruleus*) on the island of Corsica adorn their nests with fragments of aromatic plants such as lavender and thyme, which contain many of the same compounds used by humans to make aromatic house cleaners and herbal medicines[lxvii]. These substances (linalool, camphor, limonene, eucalyptol, myrcene, terpin-4-ol, pulegone and piperotenone) have antibacterial, antiviral, fungicidal, insecticidal and insect-repellent properties. Similarly, compounds in plants used for nest material have been shown to reduce the effects of fungi, bacteria and ectoparasites on falcons and starling nestlings [lxviii].

Female Great Tits (*Parus major)* also spend a good deal of time sanitising nests. If there is a heavy infestation of hen fleas they even cut down on their sleep so as to keep up with their cleaning duties[lxix]. In most cases it is only the female birds that do the nest cleaning[lxx] – if a male great tit loses its mate, the nest soon becomes contaminated with remains of food, pieces of peeling skin or even dead chicks, and the chicks are more likely to die[lxxi].

Some species even outsource their nest cleaning. Live blind snakes *Leptotyphlops dulcis*) were found in 18% of nests of Eastern Screech owls (*Megascops asio*). The snakes eat detritus and parasite larvae, which may make the owl broods healthier[lxxii].

Many species of animals thus modify their physical niches by cleaning up wastes. Some even modify their niches by influencing the behaviour of others so as to reduce the threat of infection from parasites and pathogens – not unlike the cleaning and tidying behaviour of the human animal.

From disease avoidance to disgust

The animal world presents a stunning array of behaviours that help prevent parasite invasion and infection. From selective feeding, to grooming, to frass-flinging, to outsourcing cleaning to other species or castes, it seems that every animal that has been studied has ‘parasite detecting lenses’ and commensurate parasite avoidance practices. While some of these behaviours could serve purposes other than avoiding infection, there is enough here to suggest that animals have a huge variety of infectious disease avoidance strategies. But is this disgust?

These animal behaviours are often uncannily familiar and even the language used to describe animal disease avoidance behaviour is taken from the vocabulary of human behaviour[lxxiii]. Some animals even respond in ways that look very like human expressions of disgust. In experiments using aversive tastes, lab rats (Rattus norvegicus) gape, open their mouths, gag and retch, shake their heads and wipe their chins on the floor. Coyotes (*Canis latrans*) have been seen to retch, roll on offensive food and then kick dirt over it. Some monkeys react to offensive objects by sniffing and manipulation followed by breaking and squashing the item, dropping or flinging it away and then wiping their hands[lxxiv] .

Given the overlap between what humans find disgusting and what animals avoid, and given that it probably serves the same purpose (the avoidance of infection with parasites and pathogens), should disgust be limited to humans alone?

We are so used to thinking of disgust as a *feeling* that it seems odd to suggest that animals have a disgust system, as we don't know if animals have feelings or not. But if disgust is reframed as the systems in brains that drives parasite avoidance behaviour, in whatever species, then whether animals feel disgust or not becomes irrelevant.

If the disgust function is the same does this imply that the mechanisms that animals use to detect and avoid parasite hot zones, are same as in humans? Surely not. As with all adaptive features of all animals, some are similar because they share a common ancestry (homology) and some are similar due to parallel evolution (different solutions being found to the same problem). The systems that help ants avoid their infections will have little in common with the systems that make primates avoid theirs, for example[lxxv]. Nevertheless, animals with which we share recent common ancestors, such as rats and primates, are likely to share some of the mechanisms by which we do disgust. In the near future, when we better understand its brain mechanisms and its genetic determinants it will be possible to construct a comparative phylogeny of disgust across the animal kingdom, showing what is shared and what is not, and including Homo sapiens as but one branch on the tree. Such work is in its infancy but it is exciting that it is rapidly becoming possible.

Whilst it is clear that disgust did not emerge fully formed in Homo sapiens, as many writers on the topic seem to propose[lxxvi], we might still expect human disgust to have some special features. It seems that we can use our much expanded Pre-Frontal Cortex and our ability to imagine to apply disgust more widely, (and perhaps more wisely), that can other animals. We are conscious of disgust, we have feelings about it, we are able to visualise and talk about it, we are able to learn from it, and about it, and to plan to avoid it, and we are able to weave it into our social and cultural fabric. In short, to we are able use disgust in new ways that are unimaginable to our insect, bird, mammal and primate relatives.

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