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An independent academic psychologist, based in England, who has written extensively on different areas of psychology with an emphasis on the critical stance towards traditional ideas.

A complete listing of his writings at http://psychologywritings.synthasite.com/ and http://kmbpsychology.jottit.com.

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1. PARASITE AND PATHOGEN AVOIDANCE

1.1. INTRODUCTION

Parasites, which include viruses, bacteria, fungi, protozoa, helminth worms, arthropods, and social parasites, are "more common than predators, are more diverse, contain greater total biomass, may have a greater ecological footprint and may exert a stronger selective force on their hosts than predators" (Sarabian et al 2018a p1). So, there is an incentive for hosts to develop avoidance strategies, and a host-pathogen evolutionary arms race exists. Hosts "have had to adapt to the infective strategies of parasites which track, evade detection, infiltrate, establish in, and on, and exploit hosts. Host counter-strategies include hiding from, or fleeing from, parasites and their propagules, avoiding the conspecifics and the intermediate hosts that may contain them, and avoiding foods and habitat where parasite encounter is likely. Hosts can also remove parasites directly, or engineer their own niches so as to make their environments unconducive to parasites" (Sarabian et al 2018a p2).

Animals are rarely free of external (eg: fleas) or internal (eg: tapeworms) parasites, and defensive behaviours against them are "carried out at some costs, such as reduced vigilance for predators or loss of feeding time; hence, having a manageable parasite load is adaptive in nature, representing a balance between parasite load and other physiological demands" (Hart and Hart 2018 pp1-2). Also the environment has different risks - eg: ticks in grasslands or fleas in crowded dens.

Animals live with a "parasite load", which includes "richness (the number of species of parasites present); prevalence (the fraction of parasitised individuals in a host population); intensity (the number of individual parasites in an infested host) or abundance (the number of individual parasites in a host, regardless of infestation). Thus, mean intensity is the average number of individual parasites across infested hosts in a population, and mean abundance is the average number of parasites across all host individuals, regardless of infestation" (Bush and Clayton 2018 p1).

1.2. STRATEGIES OF PATHOGEN AND PARASITE AVOIDANCE

1.2.1. Mammals

Hart and Hart (2018) presented a review of behaviours to avoid and remove pathogens and parasites by mammals. They used the following categories:

i) Biting flies - eg: a horse could be bitten by as many as 4000 tabanid flies in a day, and each bite takes blood leading to a total loss around half a litre (Hart and Hart 2018).

Ungulates avoid such flies by grouping, so the individual's encounter with flies is diluted (encounter-dilution effect; Mooring and Hart 1993). Individually, fly-repelling behaviours include head-tossing, tail switching, and ear twitching. Asian elephants, for example, swot flies with a tree branch, particularly from the areas of the body where the skin is thinner (eg: behind the ears). An experiment calculated that the use of such branches reduced the number of flies on the body by nearly half (Hart and Hart 1994).

ii) Ticks - Ticks also take blood, and this can reduce the weight gain of growing calves.

Self-grooming with the tongue is common among antelopes, for example. "Programmed grooming" is an automatic, regular process, which is influenced by the environment. For example, steinboks, which inhibit areas of vegetation (and thus have high tick risk) groom more often than klipspringers that live in rocky areas (with low tick risk) (Hart and Hart 2018).

Grooming is reduced in males by increased testosterone (eg: male impala vigilant over their females groom less and thus have more ticks) (Hart and Hart 2018).

Grooming areas of the body that the individual cannot reach themselves is achieved by "reciprocal allogrooming" (a system of exchanging grooming bouts - eg: impala). Hart and Hart (2018) described their observations (Hart and Hart 1992): "One impala approaches another in the group, often not related, and directs a bout of grooming episodes to the head or neck of the other. The partner typically reciprocates with an equivalent bout of grooming. This tit-for-tat exchange of grooming bouts continues for six to 12 exchanges. If the impala approached does not reciprocate after receiving a bout or two, the initiator walks away. One trade-off for reciprocal allogrooming is the distraction from vigilance for predators during exchanging bouts. Field tests reveal that during an allogrooming encounter the partner doing the grooming is significantly slower to notice a potential predator than is the partner receiving the grooming at the time" (p3).

Allogrooming or social grooming is common among non-human primates. Studies have shown, for example, that the most groomed baboons have less ticks, and the same for female Japanese macaques and lice (Hart and Hart 2018). But there is a cost. Vervet monkeys who groomed most had more intestinal parasites (hookworm) (Wren et al 2016). "The investigators suggest that the vervet monkeys have some faecal contamination on the fur and skin from contact with faecal-contaminated soil, and a groomer would pick up infective larvae while grooming a partner and ingest the larvae while in the process of grooming" (Hart and Hart 2018 p4).

iii) Fleas - eg: domestic cats and oral grooming with an adapted tongue to remove them, while dusky-footed wood rats place fresh bay leaves in their nests which repels fleas.

iv) Intestinal parasites - Parasitic roundworms, for example, expel eggs in faces, and so avoidance of faeces is important. Diks-diks, for instance, have been observed to selectively avoid areas near faeces (Ezenwa 2004) (appendix 1A). Some species defaecate in clumps (eg: in particular areas of a field, or away from the den and rest areas) (Hart and Hart 2018).

v) Pathogens - eg: avoid sick individuals; anti-bacterial saliva ("medicine cabinet in the mouth"; Hart and Hart 2018).

Many species show a "cannibalism taboo" - carnivores, for instance, rarely eat their own recently dead. "This would appear to be an ideal food source because the animal would be consuming a meal exactly matching the nutritional resources of their own body. But the dead conspecific may have died from an infectious disease that the animal consuming it could contract" (Hart and Hart 2018 p6).

Hart and Hart (2018) referred to the "pharmacy in the woods" to describe the use of plants by animals (eg: sick chimpanzees chewing a bitter plant known to have anti-microbial effects).

1.2.2. Birds

Bush and Clayton (2018) divided anti-parasite behaviour by birds into five broad categories:

i) Body maintenance behaviour - This includes preening with the beak, scratching with the feet [1], bathing in water or dust, and allopreening. There is also sunning (standing in direct sunlight and thereby exposing ectoparasites to ultra-violent irradiation), heterospecific cleaning (eg: birds eating ticks on mammals, but rarely situations with birds as the "clients"), and anointing or cosmetic behaviour (eg: applying pungent materials to feathers) (Bush and Clayton 2018).

Allopreening has been reported in over fifty families of birds, and it also reinforces pair bonds or hierarchies.

Table 1.1 summaries some studies that have quantified the benefits of body maintenance behaviours.

Study	Details
Waite et al (2012)	Captive pigeons experimentally infested with flies spent 24% of the time preening compared to 11% by uninfested (control) birds.
Villa et al (2016a)	Captive pigeons experimentally given feather lice spent 20% of the time preening compared to 14% for control individuals.
Villa et al (2016b)	Birds who were allopreened for less than 2% of the time had an average of 25.2 feather lice compared to 10.6 for birds allopreened greater than 2% of the time.
Cotgreave and Clayton (1994)	Long-billed species spend 16% of the grooming time scratching compared to 2% for short-billed similar species.

Table 1.1 - Four studies quantifying the benefits of body maintenance behaviours of birds.

ii) Nest maintenance behaviour - eg: "nest sanitation" (eg: eating parasites in nest); avoid larger nesting colonies where parasites can spread; "nest fumigation" (eg: placing fresh, aromatic, green vegetation in nests).

iii) Avoidance of parasitised prey - eg: oysercatchers avoid the largest cockles, which are more

[1] "Birds with long, unwieldy bills (eg: toucans) appear to be less efficient at preening than those with relatively short bills; such birds compensate for inefficient preening by scratching relatively more" (Bush and Clayton 2018 p2).

likely to contain a parasite.

Prey are often the intermediate host, and the parasite needs the definitive host (birds) to complete the life cycle, so the prey's behaviour is manipulated, like making the prey more active when birds are foraging.

iv) Migration - Escaping parasites may be one benefit of migration ("migratory escape"), while the act of migrating leads to the death of (weaker) infected individuals ("migratory culling"). Also the changes in external and internal environment is unsuitable for parasite survival ("migratory recovery") (Bush and Clayton 2018).

"On the other hand, migration may actually increase susceptibility to parasites and pathogens. The physiological stress of migration could weaken host defences. Migrants may also suffer from greater exposure to parasites as they encounter parasites on both their breeding and wintering grounds, as well as along their migratory route" (Bush and Clayton 2018 p8).

v) Tolerance - ie: compensating for parasite damage. For example, hen fleas reduced the size of individual great tit nestlings, but such individuals begged for food twice as much as individuals in unparasitised nests (Christe et al 1996).

1.2.3. Social Insects

Social insects, like ants and termites, defend themselves against micro-parasites with "social immunity" (Cremer et al 2007), which is co-operative behaviours like grooming or sacrificing sick individuals.

An important group defence is hygienic behaviour, which involves the removal of dead, dying and deceased individuals from the nest (Al Toufailia et al 2018).

Al Toufailia et al (2018) studied this inherited behaviour in the honeybee (Apis mellifera), where dead and diseased larvae and pupae are removed from sealed cells in the brood chamber as a defence against deformed wing virus, for example. The dead are removed within two days in most cases.

Social parasites are another challenge. These species (eg: slave-making ants; certain caterpillars) "directly take advantage of the sociality of their hosts" (Gruter et al 2018).

Gruter et al (2018) distinguished four types of insect social parasitism:

a) Brood parasitism (inquillinism) - a parasite queen sneaks in and lays eggs in a host's nest, and the host workers care for the brood.

b) Brood parasitism ("slave-making") - parasite queens invade a colony, and kill or expel the adults, leaving the host's brood, once developed, to care for the parasite's offspring.

c) Kleptoparasitism - stealing valuable resources, like food, from a colony.

d) Usurpation - a colony is evicted from its nest by another colony.

Social parasites are often closely related to the hosts (known as "Emery's rule").

Gruter et al (2018) outlined host defence strategies, including:

i) Avoid the parasite - eg: a queen starts a colony in an area where there are no social parasites.

ii) Nest near a parasite deterrent - eg: a stingless bee defends against a robber bee by nesting near a highly aggressive bee.

iii) Adapt the colony structure - eg: split into several smaller sub-nests.

iv) Architectural features of nest to prevent invasion - eg: decoy or false nests near to the entrance and the brood chamber hidden.

v) Improve parasite detection - eg: "entrance guards" who discriminate between nest-mates and non-nest-mates by chemical signals; change chemical profile if parasite can mimic chemical signals.

vi) Defence - eg: collective fighting; larger-bodied "warriors".

vii) Becoming unresponsive to chemical manipulation of parasites.

viii) Reduce incentive for parasites - eg: workers of stingless bee consume as much food as possible when a raid begins and regurgitates the food after the raid has ended (Gruter et al 2016).

ix) Tolerate parasites.

"Most host species do not develop a single defence trait, but use multiple defences against parasites. These sets of defence traits have been described as defence portfolios [eg: Feeney et al 2012]. Some of these defences are rather indirect and unspecific, such as being very aggressive or closing the nest entrance at night. Other traits are highly specific and directly target a particular parasite species, such as hosts that evolved unresponsiveness towards a specific manipulative secretion of a social parasite thereby becoming 'immune' to this parasites' chemical tricks" (Gruter et al 2018 p6). There is also co-evolution between parasites and hosts.

1.2.4. Aquatic Environments

Animals in aquatic environments use similar parasite avoidance behaviours to those on land in some cases, but there are also differences based on the environment (eg: parasites can be transported long distances in a relatively short period of time in water) (Behringer et al 2018). "Water is also a more hospitable and stable environment compared with air, because of its higher heat capacity, lower levels of damaging ultra-violet radiation and lack of desiccating effect. These factors likely contribute to parasite longevity outside their host" (Behringer et al 2018 p3).

Behringer et al (2018) outlined parasite avoidance behaviours in aquatic environments:

i) Detecting the risk - Hosts need to detect the risk of infection before or after the encounter with a parasite. Thus, the use of different types of cues:

a) Visual - eg: male pipefish avoid females with black spots, which is a visual cue to a parasite infection.

b) Chemical - eg: infected rainbow trout release a chemical alarm substance.

c) Auditory and mechano-sensory (vibrational).

ii) Parasite avoidance mechanisms

a) Changes in activity - eg: bursts of movement by tadpoles to fend off parasites.

b) Avoiding areas of infection risk - eg: sticklebacks preferred vegetative habitats when crustacean fish lice absent, but moved to open water when this parasite added experimentally. In the latter situation, the lice are visible in open water (Poulin and

Fitzgerald 1989).

c) Avoidance of infected prey.

d) Avoidance of infected conspecifics and mates - eg: Caribbean spiny lobsters use chemical cues to avoid lethal virus PaV1-infected individuals.

e) Group-dilution defence - eg: parasitised sticklebacks formed larger shoals and were more likely to join shoals. But, "while grouping can clearly decrease infection risk for an individual to indirectly transmitted parasites through a dilution effect, it can also increase the risk of directly transmitted infections. Heavily parasitised hosts in a group may show impaired decision-making capability because of the infection. Such behaviours could result in misguided collective movements among less-infected conspecifics, and in turn, possibly lower food acquisition rates, and raise the risk of infection or predation" (Behringer et al 2018 p12).

f) Avoidance learning - For example, Klemme and Karvonen (2016) showed learning by sea trout using a choice of two compartments marked with different colours, where one compartment was parasite-infected and the other was not. Learning took four trials on average.

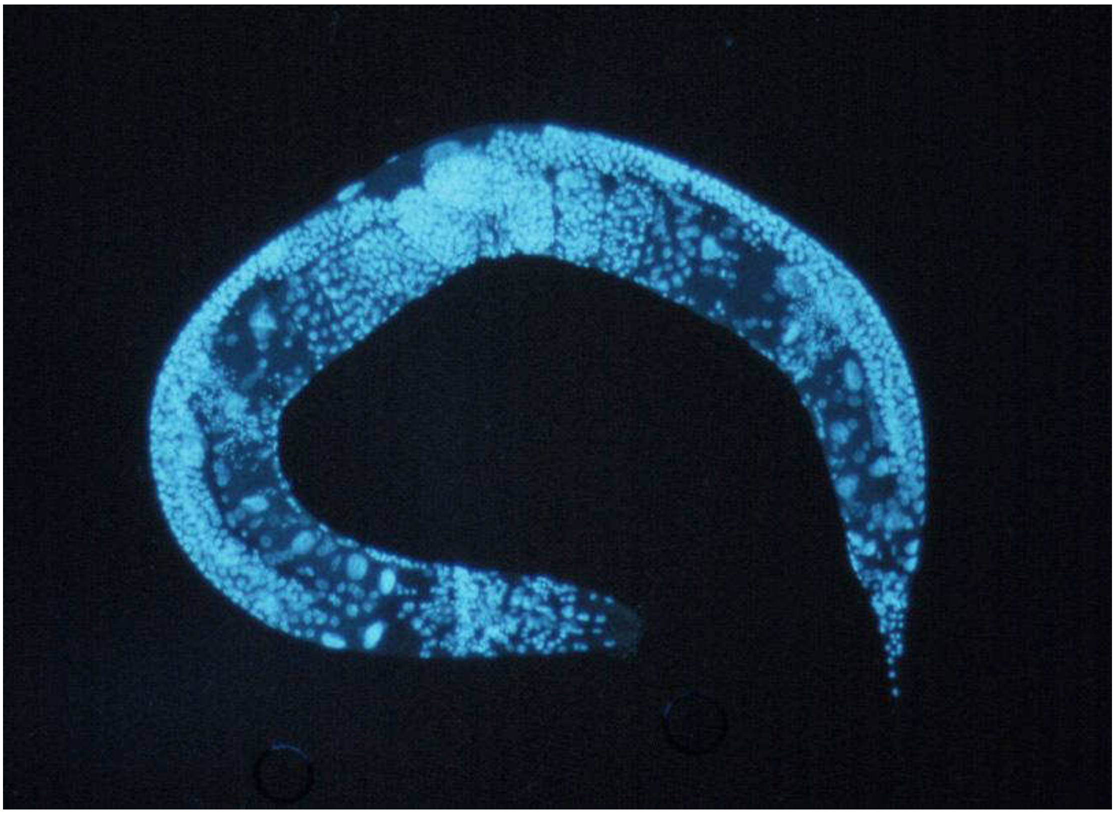
iii) Trade-offs - eg: between parasite and predator avoidance. The behaviour to avoid the parasite can increase the risk of predation. The increased activity of tadpoles to avoid parasites, say, heightens the chance of detection by predators that hunt for movement.

1.3. MECHANISMS OF PARASITE AVOIDANCE

What are the biological bases to the pathogen and parasite avoidance behaviours? A number of different organisms have been studied, but the most common invertebrate models are the fruit fly (Drosophila melanogaster) and the nematode worm (Caenorhabditis elegans) (figure 1.1) (Anderson and McMullan 2018).

The latter is popular to study with only 302 neurons and 7000 synapses, and "can be easily infected with a wide range of bacterial pathogens by providing them as a food source" (Anderson and McMullan 2018 p1).

Anderson and McMullan (2018) concentrated on contaminated food avoidance in this worm, and showed the importance of specific genes related to sensory neurons (ie: pathogen contamination detection).



(Source: National Human Genome Research Institute; https://www.genome.gov/10000570/; in public domain)

Figure 1.1 - Nematode worm.

1.3.1. Bonobos

Sarabian et al (2018b) observed that "foraging animals face a dilemma, because the same items that provide them with the nutrition and energy needed to survive and reproduce may also expose them to harmful agents that exploit such trophic interactions for their own survival and reproduction" (p1).

Concentrating on food contamination detection in bonobos, Sarabian et al (2018b) investigated the cues used in five experiments. Sanctuary-housed bonobos in the Democratic Republic of Congo were observed in response to food items placed on a table.

Experiment 1 - This experiment tested the reaction to novel food with a choice of three pieces of fruit - papaya (staple food), apple (rarely seen but eaten), and plum (novel). The bonobos chose the novel food first significantly more often, which suggested that avoiding novelty was not a strategy for dealing with the risk of contaminated food.

Experiment 2 - This experiment tested the sensitivity to contaminated food by offering three pieces of apple simultaneously - clean, covered with soil, or covered with faeces. The clean piece was chosen significantly most often first, which showed that bonobos could distinguish between contaminated and non-contaminated foods.

Experiment 3 - This experiment tested different probabilities of contamination risk using the idea of "a chain of contagion" (Tolin et al 2004). Developed in relation to therapy for contamination-related obsessive-compulsive disorder (OCD) in humans, this is the idea that a "clean" object placed with a contaminated one becomes contaminated and then passes that contamination on to other "clean" objects placed next to it.

Sarabian et al (2018b) placed six pieces of banana on a table. Slice 1 was on top of a fresh pile of faeces, and the other slices, touching each other, in a row away from that, such that Slice 6 was furthest away from the faeces. Slices further away from number 1 were chosen more often, which suggests that "bonobos can assess the probability of contamination across a set of items and use this information to inform their feeding decisions" (Sarabian et al 2018b p6).

Interestingly, nearly a quarter of bonobos refused to take any of the slices. "As the risk of parasite contamination increases in the vicinity of faeces compared with control sites, the complete avoidance of feeding near faeces may be a conservative but effective strategy to reduce parasite acquisition, particularly because the immediate surroundings of faeces are expected to be contaminated by parasites" (Sarabian et al 2018b p7).

Experiment 4 - Sarabian et al (2018b) explained that previous "experiments provided visual, olfactory as well as potential tactile and gustatory cues of the contaminant. Here, we tested whether bonobos would store information about a previous contamination event and apply this information to their feeding decisions once visual cues of the contaminant had been removed, with other cues diminished" (p8).

The bonobos were presented with two pieces of banana, one of which they had seen in contact with faeces previously. There was no difference in the choice of pieces. "This suggests that when visual cues are not maintained and other cues are diminished, contamination avoidance is not or is at best only partly triggered" (Sarabian et al (2018b p8).

Experiment 5 - This experiment tested the role of olfactory cues by presenting a piece of food in the presence of one of five odours - faeces, spoiled banana, rotten chicken (aversive smells), water or detergent (control smells). The food was placed out of direct reach, and required tool use (a stick) to obtain it.

The bonobos were significantly less likely to try to reach the food in the presence of either of the three aversive smells compared to either of the control smells.

Sarabian et al (2018b) summed up: "Across this series of experiments, bonobos showed avoidance of contaminated food items and sensitivity towards contamination-risk along a gradient of contamination probabilities. This sensitivity, however, seems to require the presence of multi-sensorial cues to enable them to associate a contamination event to a food item" (p11).

1.3.2. Social Cognition

Social cognition, which "entails the acquisition of social information about others (ie: social recognition) and from others (ie: social learning)" (Kavaliers and Choleris 2018 p1), can play an important role in parasite and pathogen avoidance.

In the case of mate choice, for instance, cognitive processes include perception of sensory cues from potential mates, recognition of differences between individuals (which includes memory for important characteristics), and decision-making in who to choose. These same processes are also involved in parasite avoidance. So, odours, which give sexual information, "can provide an index of current condition (eg: infection status and level of 'sickness')" (Kavaliers and Choleris 2018), for example.

Mice are well studied here, particularly urinary odours, with volatile elements as well as non-volatile proteins. "Using volatile components, females may be able to quickly identify the infected producer of urine marks from a distance, without having to spend time in the direct investigation of, and contact with, non-volatile cues" (Kavaliers and Choleris 2018 p4). Experiments deliberately infecting certain individuals, and then offering a female the choice of an infected and an uninfected male to mate with (eg: influenza virus; Penn et al 1998).

A social learning aspect called "mate-choice copying" (Pruett-Jones 1992) is also relevant - ie: paying attention to the mating choices of others of the same sex. "Females (observers) who witness another female (demonstrator) that was paired with a male are subsequently more likely to prefer the male (target) that was paired with the female over an unpaired male. The observer needs to recognise, select and integrate social information from the demonstrator and target and then make appropriate decisions regarding their own mate choice" (Kavaliers and Choleris 2018 p5).

A variety of neurochemicals underlie social cognition (eg: oxytocin). For example, female mice without the oxytocin gene ("knockout mice") or those given drugs that suppress it do not avoid infected individuals (Kavaliers and Choleris 2018) (appendix 1B).

1.4. HUMAN DISGUST

The emotion of human disgust evolved in relation to pathogen and parasite avoidance (Curtis and Biran 2001).

Curtis and de Barra (2018) observed that it is "unlikely to be a coincidence that many of the stimuli that elicit the emotion of disgust in humans are also implicated in the transmission of infectious disease. Human excreta, for example, are both a major source of pathogenic viruses, bacteria and helminths [eg: tapeworms] and an important elicitor of disgust. Similarly, saliva, sexual fluids, spoilt foods, ectoparasites and unhygienic behaviour are, at the same time, disgust elicitors and sources of risk of infection" (p1).

"The best strategies for avoiding pathogens would involve never opening our mouths, never opening our eyes, and never touching another person" (Tybur and Lieberman 2016 p7). Obviously, individuals would not survive behaving like this, so there is a trade-off of risks and benefits. For example, kissing risks transmission of pathogens, but the reproductive benefits associated with it outweigh the cost.

There are two potential errors of any pathogen detection system - false alarm (false positive/type I error) and miss (false negative/type II error). The former is rejection of a food which is not harmful, for example, while the latter is eating the spoiled food. The cost of the miss is greater (eg: death). However, the human emotion of disgust is not an accurate "measure" of pathogen risk as "people often do not experience disgust toward some substances that house pathogens, such as a cooked hamburger that secretly houses Escherichia coli bacteria, and they also sometimes experience disgust toward objects that are free of pathogens, such as fudge that is shaped to look like faeces" (Tybur and Lieberman 2016 p6).

Based on students' listings, Haidt et al (1994) distinguished seven types of disgust-related items - death; hygiene; animals; body wastes; sex; "sympathetic magic"; "body envelope violations and foodstuffs. These categories have been reduced to three, subsequently - "core disgust", "animal disgust", and "contamination disgust" - in the Disgust Scale-Revised (DS-R) (Olatunji et al 2009).

An alternative is the Three Domains Disgust Scale (TDDS) (Tybur et al 2009), whose three categories/domains are linked to three evolutionary adaptation problems - "pathogen disgust" (linked to preventing infection), "sexual disgust" (mate choice), and "moral disgust" (regulating others' social behaviour by avoidance, say) (Curtis and de Barra 2018).

Curtis and de Barra (2018) took a different approach, arguing that human disgust is linked to the main transmission pathways for pathogens:

- Direct interpersonal contact (eg: yaws transmitted by skin to skin contact);

- Interpersonally through droplets in the air (eg: sneeze);

- Interpersonal sexual contact;

- Contact with secondary host (eg: rats);

- Ingestion of contaminated food or liquid;

- Contact with fomite (a pathogen-contaminated object).

Over 2600 online participants (two-thirds from the UK) were asked to rate seventy-two scenarios based on the above modes of transmission on a 100-point scale (table 1.2).

- A stray dog licks you on your face.
- You see some unflushed excrement in a toilet.
- You accidentally use someone else's roll-on deodorant.
- Shaking hands with a homeless man.
- Finding a furry green patch on a loaf of bread.
- Seeing pus coming from a genital sore.

(Source: Curtis and de Barra (2018) table 1)

Table 1.2 - Examples of scenarios used by Curtis and de Barra (2018).

Factor analysis of the responses produced six cues for disgust:

i) Hygiene - displays/physical evidence of unhygienic behaviour.

ii) Animals/insects - eg; mice (disease vectors).

iii) Sex - "pertaining to promiscuous sexual activities", but not symptoms of sexually transmitted diseases, which appeared under "lesions".

iv) Atypical appearance - "infection cues in other people" (eg: deformity), behaviours (eg: coughing), and high risks (eg: homelessness).

v) Lesions - signs of infection on the body (eg: blisters, pus).

vi) Food - signs of spoilage.

Curtis and de Barra (2018) stated: "These results partially supported our initial prediction that different kinds of disgust would reflect the different transmission routes of infectious disease, but they also departed from our prediction in an interesting way. It appears that cues to infectious disease threats are not categorised following the abstract biomedical categories of disease transmission risk recognised in the literature (interpersonal by contact, sexual activity or droplet, vectors, ingestion, fomite), but, rather, as categories of recognizable cues as to what to avoid. These include potentially contaminated objects such as bodily fluids, infected lesions, spoilt foodstuffs, and animals that vector disease, practices such as those who run the risk of contracting sexually transmitted diseases, and people who display visible signs of disease or poor hygiene" (p13).

Women tend to be more easily disgusted than men, which fits the evolutionary explanation. "In our evolutionary past, it tended to be mothers who looked after the children, so it really paid for them to be extra squeamish because they had to not get sick themselves. They also had to keep young, dependent children safe. Having an extra disgust towards food, for example, or if there was a sick person around who was going to make your child sick, you would perceive that a little more carefully" (Curtis quoted in Saner 2018).

Other researchers (eg: Frederick et al 2018) have found that individuals who are highly sensitive to disgust are more risk aversive generally (and vice versa) (Saner 2018).

The emotional responses to disgust has evolutionary advantages, as Tybur et al (2018) outlined: "The facial movements that accompany disgust limit the degree to which the surface of the eye is exposed to those pathogens that infect via sprays of liquid from an already infected individual; notably, the reduced surface area of the eyes has alternatively been interpreted as functioning to increase visual acuity so that potentially pathogenic substances can be better examined). If sensory cues to pathogens are detected in the mouth (eg: via taste perceived as disgusting), then the tongue expels them; if pathogen cues are detected via olfaction, then the lips clench to prevent oral incorporation. And, perhaps most importantly, disgust motivates the avoidance of physical contact with the disgust elicitor—exactly the type of contact that would transmit pathogens" (p2).

1.4.1. Grooming

Disgust is a defence against ingested parasites and pathogens, but is less effective for ectoparasites (which attach to the body surface). Kupfer and Fessler (2018) argued that humans, like other animals, have a separate ectoparasite defence system. "A distinct ectoparasite defence adaptation that guards the body surface might therefore increase fitness beyond the protection afforded by pathogen disgust. Such an adaptation would be expected to have mechanisms that detect ectoparasites, increase vigilance to the body surface, potentiate skin sensations such as itch, and prepare active defence behaviours, including grooming movements" (Kupfer and Fessler 2018 p2).

Among non-human animals, grooming is a common strategy, but it is costly in terms of energy expended, wear and tear (eg: hair loss; saliva depletion), and loss of foraging time and ability to detect predators and rivals (Kupfer and Fessler 2018). Therefore, grooming must be effective. For example, chickens unable to preen (due to beak removal) had twenty times the number of lice than beaked chickens after one month (Brown 1972).

Grooming is divided into "stimulus-response" (or stimulus-driven) grooming (eg: immediate response to ectoparasite bite) and "programmed" grooming (or "scratch and scan" grooming) (ie: periodic bouts of grooming each day) (Kupfer and Fessler 2018). Kupfer and Fessler (2018) stated: "Although humans may not perform a stereotypical chain of grooming movements akin to those evident in mice, we suggest that, like non-human animals, humans have both stimulus-driven and programmed forms of grooming" (p4).

Stimulus-response grooming increases in experiments showing pictures of ectoparasites (eg: video of head lice and itchy sensation; Ogden and Zoukas 2009). This also shows the "contagious itch" (ie: watching others scratch increases the itching sensation), including activation of certain brain regions (called the "itch matrix") (Kupfer and Fessler 2018).

The human ectoparasite defence system can also be seen in its disorders - eg: trichotillomania (skin picking) and programmed grooming; entomophobia (fear of insects) and stimulus-response grooming (Kupfer and Fessler 2018).

1.4.2. Individual Differences

Tybur et al (2018) explored individual differences in human disgust (ie: disgust sensitivity) in relation to the three main possible explanations:

i) Disgust sensitivity is related to emotionality (or neuroticism) on personality scales - eg: a positive correlation between scores on the Disgust Scale and the Eysenck Personality Questionnaire (Haidt et al 1994).

However, the strength of the relationship varies between studies, and Tybur et al (2018) highlighted methodological issues, like the measurement of disgust (eg: "It would bother me to see a rat run across my path in a park"). Clark and Watson (1995) stated that such wording "virtually guarantees that an item will have a substantial neuroticism component; the inclusion of several such affect-laden items, in turn, ensures that the resulting scale — regardless of its intended construct — will be primarily a marker of neuroticism" (quoted in Tybur et al 2018).

Tybur et al (2018) drew the following conclusion: "(1) disgust sensitivity is not a component of neuroticism/emotionality; (2) the validity of inferences based on the use of disgust sensitivity instruments (perhaps with the exception of the Disgust Scale and Disgust Scale–Revised) is unlikely to be compromised by confounds with neuroticism/emotionality; and (3) neuroticism/emotionality and disgust sensitivity likely have different genetic and environmental roots" (p3).

ii) The role of parental modelling in early life (socialisation hypothesis) - Two lines of evidence are offered here:

a) The experience of disgust does not appear until five years old, so plenty of time to observe parents' behaviour.

In response, Tybur et al (2018) quoted this analogy: "traits such as teeth, beards and breasts are absent at birth but reliably develop independently of the environmental inputs that would be classified as 'socialisation'" (p4).

b) Parents and offspring have similar scores on measures of disgust.

But this could be a product of shared genes as much as socialisation. In a Finnish twin study, for example, Sherlock et al (2016) found that the correlation on pathogen disgust sensitivity was higher for identical than non-identical twins, which suggested that shared genes were important.

iii) Earlier experiences with pathogens - Two predictions emerge from this explanation that greater early contact with pathogens leads to greater disgust sensitivity (Tybur et al 2018):

a) Nations that differ in infectious diseases in the young will differ in disgust.

In a study of over 11 000 individuals in thirty countries, no relationship was found between national infectious disease and disgust sensitivity (Tybur et al 2016).

b) Individuals who are less able to resist pathogens will have greater disgust sensitivity.

Not supported by the evidence (eg: Bangladesh; De Barra et al 2016).

Tybur et al (2018) offered three other factors that need further study in explaining individual differences in disgust:

- Current and expected future availability of calories.

- Co-operative contact between humans. For example, "individuals with social orientations that involve more physical contact might invest more attentional resources in detecting pathogens rather than motivations to avoid them" (Tybur et al 2018 p8).

- The evolution of monogamy as a sexual strategy - eg: "more-pathogen-avoidant individuals being more socio-sexually restricted (ie: less open to sex outside of a relationship" (Tybur et al 2018 p8).

Ultimately, Tybur et al (2018) did not have a clear explanation for the individual differences in human disgust.

1.4.3. Political Attitudes

"Evolutionary political science" (Lopez and McDermott 2012) applies the principles of evolutionary psychology to understand political views.

Generally, two key dimensions in political attitudes have emerged - advocating social change - tradition (left - right wing ideology), and advocating equality - inequality (Tybur et al 2015a).

Advocating for tradition (or conservatism) has been linked to pathogen avoidance. "For individuals who are more invested in avoiding pathogens, the reasoning goes, the putatively pathogen-mitigating aspects of right-wing ideologies make these ideologies more appealing" (Tybur et al 2015a p489). Terrizzi et al's (2013) meta-analysis, for example, found an average correlation of r = 0.26 between pathogen avoidance (eg: disgust sensitivity) and political conservatism. It is argued that pathogen avoidance can be improved by behaviours which are associated with conservatism, like preference for traditions, and strong ingroup favouritism/outgroup discrimination (Tybur et al 2015a).

Tybur et al (2015a) preferred to see this relationship as a product of sexual strategies. Differences in pathogen avoidance between individuals leads to different sexual strategies, and consequently to differences in attitudes. For example, highly pathogen-avoidant individuals (with high disgust sensitivity, for instance) are less open to sex outside of a monogamous relationship, and so are against "non-traditional" activities that encourage casual sex (eg: drug use). "Therefore, individuals following relatively monogamous mating strategies have a strategic interest in endorsing rules proscribing sexual promiscuity – rules that characterise many ideological aspects of social conservatism" (Tybur et al 2015a p490).

Tybur et al (2015a) reported three studies of this idea.

Study 1 - 819 US adults recruited via Amazon Mechanical Turk (MTurk) completed the Three Domain Disgust Scale (TDDS) (Tybur et al 2009), which has twenty-one items covering disgust related to pathogens [2], sex [3], and morality [4]. Political attitudes were self-reported by three questions, including last voting choice (ie: Republican or Democrat). The sexual disgust items of TDDS [5] were found to have the strongest relationship to conservatism/Republican voting.

Study 2 - With 238 more MTurk-recruited individuals, a wider variety of measures of disgust and tradition were used. The findings from Study 1 were confirmed.

[2] Eg: "Accidently touching a person's bloody cut".
[3] Eg: "Hearing two strangers having sex".
[4] Eg: "Intentionally lying during a business transaction".
[5] Eg: "Bringing someone you just met back to your room to have sex".

Study 3 - 254 more participants completed more measures of pathogen avoidance and conservatism. As with the other studies, the researchers "observed no direct effect of pathogen avoidance on ideological conservatism. That is, any relationship between pathogen avoidance and conservatism was fully mediated by sexual strategies, regardless of which of two instruments of pathogen avoidance were used, and which of two instruments of sexual strategy was used" (Tybur et al 2015a p494).

Shook et al (2015) criticised Tybur et al's (2015a) work in three ways:

i) Theoretically - Pathogen avoidance is not just related to sexual behaviour, but is a greater risk from general contact with other people. Thus, it would make more sense evolutionarily to shun strangers generally (ie: prejudice) rather than just sexually.

ii) Methodologically - The validity of the TDDS was questioned. For example, one item, "performing oral sex", measures disgust towards the sexual act, not disgust of promiscuity. The self-reporting of political attitudes based on three questions was also criticised.

iii) Data analytics - Tybur et al (2015a) used statistical modelling which Shook et al (2015) described as "overly complex".

Shook et al (2015) also performed a replication of Tybur et al's (2015a) work with 381 US individuals. These researchers found that pathogen avoidance was directly associated with conservatism.

Tybur et al (2015b) refuted the above criticisms. They argued that the original three studies (and two unpublished data sets) supported "the fact that (1) pathogen disgust does not relate to social conservatism independent of sexual disgust in five samples..., and that (2) sexual strategies fully mediate (in our five samples) or partially mediate... the relationship between pathogen avoidance and social conservatism across a range of operationalisations of all three constructs" (Tybur et al 2015b p504).

Lee et al (2015) linked sensitivity to pathogen prevalence to aspects of mate choice. In particular, low waist-to-hip ratio (WHR) of women (ie: "the circumference of the waist measured at its narrowest point, divided by the circumference of the hips measured at their widest point"), high men's shoulder-to-hip ratio (SHR) (ie: "the relative size of the shoulders compared to the hips"), and lower body mass index (BMI) generally signal health.

In their first study, Lee et al (2015) asked 252 males and 238 females recruited online to rate oppositesex, computer generated bodies, and complete the TDDS. It was found that men with higher pathogen disgust sensitivity had a significantly greater preference for female bodies with lower WHRs, but there was only a non-significant relationship between female higher pathogen disgust sensitivity and preference for higher SHR male bodies. There was no relationship between pathogen disgust and BMI preference.

In a second study, the researchers presented 138 male and 124 female online participants pairs of computer-generated bodies to choose the more attractive. It was found that "men higher in pathogen disgust preferred lower WHR, while women higher in pathogen disgust preferred higher SHR" (Lee et al 2015 p485).

1.4.4. Body Odour Disgust

Disgust is "a pervasive emotion that might have... evolved as a defence mechanism to protect the body from contamination by potentially harmful substances" (eg: pathogens and disease) (Liuzza et al 2018 p2). But disgust may also be involved in prejudice. For example, Faulkner et al (2004) found a correlation between higher perceived vulnerability to disease, and negative attitudes towards unfamiliar outgroups.

Liuzza et al (2018) summed up the research: "In fact, feelings of disgust have been consistently linked to the stigmatisation of ethnic and sexual minorities. On a cross-national level, the risk of being exposed to parasites was associated with cultural differences in the endorsement of traditional values, conformism and in the emphasis on the psychological distinction between ingroup and outgroup. From a BIS [behavioural immune system] perspective, prejudice can be seen as a social discriminatory behaviour partly motivated by the fact that pathogens represent an invisible threat and individuals with high levels of disgust sensitivity might be more likely to avoid foreign people, and to promote policies that avoid contact with them, because they are perceived as potentially spreading unfamiliar pathogens, or different hygienic or food habits" (p2).

Liuzza et al (2018) concentrated on body odour disgust sensitivity [6], and the hypothesis that higher levels of it (ie: more disgusted by body odour) would be associated with authoritarian attitudes (ie: prejudice). The researchers performed three studies.

Study 1 - Two hundred and one participants were

[6] Traditionally, measures of disgust, like the Disgust Scale-Revised (DS-R) (Olatunji et al 2007) have paid little attention to olfactory disgust (Liuzza et al 2017).

recruited in April 2013 via the Internet (MTurk) [7]. They completed the Body Odour Disgust Scale (BODS) (Liuzza et al 2017) [8], which involves twelve scenarios (table 1.3) rated as "not disgusting at all" (1) to "extremely disgusting" (5). The participants also completed measures of political and moral attitudes (eg: "There are many radical, immoral people trying to ruin things; the society ought to stop them"; "Facts show that we have to be harder against crime and sexual immorality, in order to uphold law and order"). BODS scores were found to be related to right-wing authoritarian political attitudes.

- You are alone at home and notice that the T-shirt you are wearing smells strongly from your own sweat.
- You are sitting next to a stranger and notice that their feet smell strongly.
- You use the bathroom after a stranger and notice that the room smells strongly of their urine.

(Source: Liuzza et al 2017 table 2 p502)

Table 1.3 - Example of items on BODS.

Study 2 - This study involved 157 US participants recruited via MTurk in March 2015, who completed similar measures to Study 1. The findings from that study were replicated.

Study 3 - This study in October 2016 involved 391 MTurk-recruited US participants. As well as the previous measures, attitudes towards Donald Trump were measured. High BODS scores were associated with positive attitudes towards Trump.

Liuzza et al (2018) summed up: "Our findings suggest that high reactivity to pathogen threats signalled by body odours is part of an ideological disposition towards authoritarian candidates, because of the link between disease avoidance and authoritarianism" (p15).

The samples were individuals who visited the MTurk website (table 1.4) [9] [10], and they were paid a small fee to

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7 Known as "crowdsourcing" - ie: "accessing large numbers of participants from the Internet" (Litman et al 2017).

8 The initial BODS covered seven types of body odour - breath, upper body sweat, feet, faeces, urine, genitals, and gas - each presented in five contexts - own-smell alone at home, own-smell near a friend/partner, own-smell near an unfamiliar person, smell of a friend/partner, and smell of an unfamiliar person. After the responses of 528 participants, this was reduced to the final twelve items (Liuzza et al 2017).

9 Amazon Mechanical Turk began in 2005 as a way to recruit individuals for particular (labour-intensive) jobs (ie: "online labour market"). "Workers" (employees) are recruited by "requesters"

Advantages	Disadvantages
1. A large amount of data easily collected from geographically distributed/culturally diverse individuals. 2. Fast recruitment (eg: 1000 participants in three weeks; Paolacci et al 2010) 3. More diverse than student-based samples (Liuzza et al 2018). 4. Valid for research on political attitudes (Clifford et al 2015). 5. Interactive-based research is possible as many users active at same time (Paolacci et al 2010). 6. Participant anonymity (ie: website ID number only known), but continued/longitudinal research possible based on ID number. 7. Specific samples possible (eg: women only). 8. "Contaminated subject pool" low risk (ie: past participants telling future participants about the study). 9. Multiple responses by one person low because of ID number. 10. No risk of experimenter effects as in laboratory/face-to-face studies.	1. Different to general population (Paolacci et al 2010). 2. Motivation to visit site is usually to earn money from work, so low motivation for study compared to laboratory-based study. 3. Not a random sample. 4. Data quality as participants paid so little (eg: $0.10). 5. General web survey problem of "unsupervised" completion of questionnaire (eg: little attention to questions). 6. Not sure if participant has performed similar type of task beforehand. 7. "Workers" may share information about the study on blogs, including unhappiness about pay. 8. The right to withdraw after agreeing to perform task versus no longer naive for future similar studies. 9. Cultural diversity is limited by computer ownership and use. 10. Individuals generally give different answers when they know anonymous compared to when identifiable. Also general issue of honesty.

Table 1.4 - Advantages and Disadvantages of the Use of "Amazon Mechanical Turk" samples.

(employers) for HITs (human intelligence tasks) for reward ("wage") anonymously (Paolacci et al 2010).

[10] Because MTurk was not designed for research purposes, Litman et al (2017) developed the TurkPrime Data Acquisition Platform for the Social Sciences (TurkPrime) to use with MTurk. It allows greater control over who participates in a study including the facility for longitudinal and panel studies.

complete the questionnaires ($0.50). BODS was measured by a self-reported scale rather than reaction to actual smell.

Paolacci et al (2010) collected data on the demographics of 1000 "workers" on MTurk in February 2010 with a three-minute survey (for a $0.10 reward). Around half of the respondents were US-based, and one-third from India. Among the US group, two-thirds were female, and the average age overall was 36 years old (younger than the general US population). The education level was higher than the general population, but average income was self-reported as lower.

Paolacci et al (2010) also compared the responses to three judgment tasks of a sample from MTurk (n = 131 US-based) with those of visitors to several psychology-based online discussion groups (n = 137), and students at a US university (n = 141) in early 2010. The three groups showed similar choices.

1.5. APPENDIX 1A - HERBIVORES

Mammalian herbivores risk infection by gastrointestinal parasites transmitted via faeces on the ground, which leads to suppression of appetite and associated consequences ("parasite-induced anorexia") (Coulson et al 2018).

But not all individuals are affected in the same way. Beldomenica and Begon (2010) proposed the idea of a "vicious circle" - ie: "a positive feedback loop between body condition and parasite infection: poor condition predisposes individuals to infection, which then reduces the condition of the host, further predisposing the host to infection" (Coulson et al 2018 p6).

A common strategy for domestic sheep and cattle, say, is "to avoid faeces while foraging, thereby reducing their risk of ingesting infective larvae on the surrounding pasture. Paradoxically, this avoidance behaviour creates patches of pasture that are taller, due to reduced offtake, and more nutritious, due to the fertilising action of faeces. Foraging hosts then face a trade-off between the risks of acquiring parasites and the benefits of foraging in the most nutritious patches" (Coulson et al 2018 p2).

Garnick et al (2010), for example, observed that Eastern grey kangaroos took fewer bites of ground vegetation in areas of greater faecal contamination. Ezenwa (2004) offered dik-diks food placed adjacent to faeces or not, and the animals took over four times more bites from the uncontaminated food.

Lieberman et al (2018) argued that disgust evolved to deal with three separate adaptive problems:

1. What to eat.

Threats from food are mechanical (eg: extreme temperature), chemical (plant-based toxins), and biological (eg: pathogens) (Lieberman et al 2018).

All the senses are involved in biological threats, but chemical threats provide less cues. "The general lack of direct cues to the toxicity of food (apart from bitter-tasting alkaloids) may promote human reliance upon socially transmitted information regarding which plant species may be safely consumed" (Lieberman et al 2018 p3). For example, infants watching an adult show disgust at a piece of food expected other adults to do the same (Liberman et al 2016).

Nutritional state also influences the disgust response. For example, thirsty men reported less disgust to the smell of fermented fish than well-hydrated participants (Meier et al 2015). This is the response to micro-organism presence, but depleted individuals become more negative towards toxin presence. Thirsty individuals were more likely to refuse quinine-containing liquids than non-thirst ones (Stevenson et al 2010). The bitter taste of quinine is taken as a cue of toxin presence. "So whereas the consumption system relaxes its objection to items harbouring micro-organisms, probably in a very controlled manner, it intensifies its objection to toxins. Better to risk illness from which one can recover, than death" (Lieberman et al 2018 p4).

Other factors involved in disgust towards food include prior experience, and developmental stage (eg: pregnant women more disgust sensitive) (Lieberman et al 2018).

2. What to touch.

Lieberman et al (2018) stated: "we suspect that, in the human psychological architecture (and probably in the architecture of many other species), there exists a system that takes as input cues associated with the presence of micro-organisms on conspecifics, other animals and surfaces in general, and then computes for a given surface the probability of pathogen presence" (pp5-6).

Chimpanzees, for example, recoiled if their hand unexpectedly touched a piece of dough when reaching for a banana slice (Sarabian et al 2017).

Physical contact with kin produces less disgust than with a stranger. "Despite the very same physical properties, our brain appears to use information regarding relatedness to regulate our perceptions of the costs versus benefits of contact" (Lieberman et al 2018 p6). Co-operative non-kin relationships are the same.

3. With whom to have sex.

There is less disgust related to an attractive potential sexual partner (ie: "expected sexual value"; Tybur et al 2013).

Sexually aroused men, for instance, reported less disgust towards sex-related stimuli than non-aroused individuals (Stevenson et al 2011).

The expected sexual value guides decisions on whom "to pursue, accept and avoid as a sexual partner for oneself" (Lieberman et al 2018). The process involves an assessment of "mate value", and of relatedness. Gender, one's own mate value, and availability of potential mates are also relevant. "When elevated, expected sexual values generate a sense of sexual attractiveness and motivate sexual pursuit. When low, expected sexual values cause avoidance behaviours and give rise to our sense of disgust" (Lieberman et al 2018 p8).

1.6. APPENDIX 1B - OXYTOCIN

Oxytocin (OT) is a hormone produced by the hypothalamus, which has been linked to maternal behaviour. OT administration studies, where individuals inhale OT, for instance, have found various effects, including (Gangestad 2016):

- Increased brain activity in reward-related areas when viewing infants or sexual stimuli.

- Similar effect in male brain to viewing photographs of partner.

- Increased compassion by both sexes towards women, but not towards men.

- Women perceive other women's faces as showing more warmth, while men see less warmth in other men's faces (compared to placebo).

There are many and varied consequences to increased OT, then, but what is the overall purpose of the hormone? One theory is as a "love molecule" (eg: Zak 2012) promoting bonding and pro-sociality. However, Bethlehem et al (2014), for instance, found self-serving or aggressive responses to OT administration.

The "social salience hypothesis" (Bartz et al 2011) suggested that OT "sharpens focus on social events in general, such that its effects (eg: pro-sociality versus aggression) depend on the nature of social information (eg: whether it invites trust or threaten harm)" (Gangestad 2016 pp115-116).

Gangestad (2016) challenged OT administration studies from an evolutionary viewpoint - "OT infuses neural circuits under circumstances a researcher chooses, not when selection designed the organism for it to happen. Before the study, no human may have experienced OT infusion under those circumstances. OT's effects in the study may not accurately convey how OT affects behaviour in circumstances naturally leading to OT release" (p116).

He argued that OT evolved in humans to support pair-bonding. For example, Schneiderman et al (2012) found that "new lovers" each had very high OT levels. But Taylor et al (2010) found higher OT levels in women who reported non-response and uninvolved partners.

"Might, then, OT levels rise when individuals are highly involved in their relationships, but their partners are much less involved?... OT may function to foster the development or maintenance of romantic relationships at risk. Again, the precise psychological effects of OT remain debated. But one possibility is that OT affects motivational systems. An individual motivated to protect and enhance a targeted relationship that is at risk may track the partner's needs, seek to respond to the partner's needs, and so on" (Gangestad 2016 p117).

He added: "The function of OT in mother–infant contexts may be understood similarly. Infants are, by their nature, at risk and dependent upon caregiver responsiveness. Once again, these effects may have been co-opted to function in pair-bonds and perhaps other important social relationships" (p117).

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2. ARCHITECTURE AND BEHAVIOUR

2.1. INTRODUCTION

Physical structures of the environment influence interactions between individuals and emergent collective behaviour, whether that be social insects and nest architecture, or modern buildings and humans (Pinter-Wollman et al 2018a).

"To study the impact of architecture on collective behaviour, it is necessary to quantify the built environment and the movement patterns inside these built structures that result in the interactions that underlie the emergence of collective behaviours" (Pinter-Wollman et al 2018a p2). That includes the physical structures themselves (eg: arrangement of buildings; design within the building), features of the structures (eg: noise, smell), or the connectivity of these things (eg: "space syntax"; Hillier and Hanson 1984).

There is also the movement patterns within and between structures. "Built structures constrain the movements of the organisms inhabiting them, thus impacting the flow of information, ideas and disease" (Pinter-Wollman et al 2018a p4).

2.2. BUILT ENVIRONMENT AND DISEASE

"The built environment can affect health directly and indirectly either through immediate, passive impact (eg: effects of indoor environmental quality) or by influencing behaviours that can affect health, which can involve individuals' active participation (eg: encouraging walking to increase physical activity" (Pinter-Wollman et al 2018b p2).

Cities in the 19th century, for instance, contributed to epidemics of infectious diseases by their overcrowding, while the reaction to this with "zoning and development of suburbs, along with the advent of the automobile, led, 100 years later, to environments that discourage walking and promote movement in the private automobile. We now have a physically inactive population with rising rates of obesity and related chronic diseases such as diabetes, cancer and coronary heart disease" (Pinter-Wollman et al 2018b p2).

Pinter-Wollman et al (2018b) outlined different ways in which the built environment has impacted on chronic and infectious diseases:

i) Prevention of chronic diseases - eg: neighbourhood design that is pedestrian- rather than car-focused, and thus encourages physical activity; "placing a stairway in a salient location and making it inviting and aesthetically pleasing, while locating elevators in a less obvious, less central position, may encourage stair use" (Pinter-Wollman et al 2018b p3).

In terms of diet, Bodor et al's (2010) study of 3000 New Orleans residents found that additional supermarkets in the locality reduced the likelihood of obesity, while additional fast food restaurants and convenience stores increased the risk.

ii) Therapeutic design - eg: "views of and access to nature have been linked to a wide variety of health outcomes" (Pinter-Wollman et al 2018b p6).

iii) Prevention of infectious disease - eg: hospital building air cleaning and ventilation that dilutes airborne pathogens, like influenza, and control their movement; "the choice of building materials and coatings of indoor surfaces, such as walls, floors and furniture, can decrease the survival of pathogens and ease cleaning and sterilisation" (Pinter-Wollman et al 2018b p8).

iv) Containment of infectious disease - eg: quarantine.

2.3. WORK ENVIRONMENTS

Lindberg et al (2018) studied 248 office workers in four US government office buildings with a small, chest-worn, cardiac activity sensor, and an accelerometer sensor for a week, along with a questionnaire about perceived stress. Three types of workstation were assessed - private office, cubicle, and open desks/benches.

The latter group had the highest amount of physical activity during a day in the office (about one-third higher than private office workers and 20% higher than cubicle-based employees).

Workers on open desks/benches reported significantly lower perceived and physiological stress than the other two types.

Lindberg et al (2018) commented: "Workers tend to rate private offices as more desirable than other office workstation types, but there may be other consequences when compared with open bench seating arrangements. For instance, valuable, impromptu conversations may be an unintended benefit to this design strategy, as well as improved communication and an increased awareness of others. It is possible that the open nature of a space leads to increased physical activity by encouraging interaction and mobility, including movement to spaces designed for unplanned meetings and phone calls, when available. Individuals in open bench seating may also be more aware of others and more dependent on shared services (eg: meeting rooms, printing and filing areas, social spaces) than those in private offices" (p5).

Bernstein and Turban (2018) studied the interactions of 52 staff members in the global headquarters of a large US company, which had changed to an open-plan office. Staff members wore a sensor which recorded the direction of facing, a microphone, and an accelerometer to measure movement. Data were collected for fifteen days and compared to the previous situation when the floors were divided into small offices.

Surprisingly, face-to-face interactions declined by three-quarters with the open-plan office, and virtual interactions increased (over 50% more emails).

Bernstein and Turban (2018) replicated this finding in the study of another large US company which moved from individual cubicles to open-plan design.

2.4. ANIMALS

Smith et al (2018) noted that it is becoming "increasingly clear that who-meets-whom within animal societies is rarely random and that social structure is often produced by individual variation in social preferences within groups" (p1).

According to social network theory (eg: Wey et al 2008), repeated interactions between pairs of individuals eventually leads to social structures. Social structures function on "three major, non-mutually-exclusive mechanisms" (Smith et al 2018):

- "Movement rules" - encounters between individuals in the daily travel to and from limited resources.

- "Social interaction rules" - eg: the tendency for similar individuals to choose to interact (known as "homophily"; McPherson et al 2001).

- "Individual characteristics".

Smith et al (2018) examined these mechanisms in a study of the California ground squirrel at a field site in California. Individuals were tagged and their movement below-ground was monitored by radio-frequency identification. Above-ground social behaviour was scored by human observers. The study took place for two months in 2016 and 2017, and included a total of around 300 observation hours of over 100 individuals.

Below-ground interactions between individuals correlated with above-ground affiliative networks: "That is, pairs that occupied burrows at the same location on the same days were significantly more likely to exchange affiliative behaviours above-ground than were pairs that rarely visited similar burrows. This finding is consistent with the notion of movement rules because individuals seeking safety at similar burrow complexes (home bases) were presumably also most likely to encounter each other above-ground as they moved towards or away from these refuges" (Smith et al 2018 p7).

The squirrels did not show homophily as "individuals tended to associate most often with individuals belonging to a life-history stage different from their own" (eg: juvenile-adult pairs) (Smith et al 2018 p7).

In relation to "individual characteristics", Smith et al (2018) found that "some individuals consistently occupied key positions in social networks across time (personalities) and major ecological contexts (behavioural syndromes)" (p8). This conclusion was based on the observation of a sub-set of nineteen individuals in both years of the study.

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