Ectoparasite defence in humans: Relationships to pathogen avoidance, and clinical implications

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Summary

Currently, disgust is regarded as the main adaptation for defence against pathogens and parasites in humans. Disgust's motivational and behavioural features, including withdrawal, nausea, appetite suppression, and the urge to vomit, defend effectively against ingesting or touching sources of pathogens. However, ectoparasites do not attack their hosts via ingestion, but rather actively attach themselves to the body surface. Accordingly, by itself, disgust offers limited defence against ectoparasites. We propose that, like nonhuman animals, humans have a distinct ectoparasite defence system that includes cutaneous sensory mechanisms, itch-generation mechanisms, and grooming behaviours. The existence of adaptations for ectoparasite defence is supported by abundant evidence from nonhuman animals, as well as more recent evidence concerning human responses to ectoparasite cues. Several clinical disorders may be dysfunctions of the ectoparasite defence system, including some that are pathologies of grooming, such as skin picking and trichotillomania, and others, such as delusory parasitosis and trypophobia, which are pathologies of ectoparasite detection. We conclude that future research should explore both distinctions between, and overlap across, ectoparasite defence systems and pathogen avoidance systems, as doing so will not only illuminate proximate motivational systems, including disgust, but may also reveal important clinical and social consequences.

The literature on pathogen and parasite avoidance in humans identifies the emotion disgust as the adaptation of principal importance[1–5]. Disgust is well suited to pathogen (i.e., infectious microorganism) avoidance, as cues to the presence of pathogens motivate avoidance of consumption or contact[6,7]. However, ectoparasites do not gain access to their host via incorporation, but rather by attaching themselves to the host's body surface. Therefore, although disgust can function effectively to defend against pathogens that enter the host via the oral pathway, by itself it offers limited defence against ectoparasites. We propose that, like nonhuman animals, humans have distinct adaptations for ectoparasite defence, including cutaneous sensory mechanisms, itch-generation mechanisms, and grooming behaviours. We review evidence for the existence of these mechanisms, and suggest that their operation is most dramatically revealed in certain clinical disorders, including trichotillomania and delusory parasitosis. We examine relevant evidence on ectoparasite defence in nonhuman animals, as well as recent evidence concerning human responses to ectoparasites, and make recommendations for future research.

1. Form and function

Disgust has several properties that identify it as an adaptation serving the function of pathogen avoidance, including feelings of revulsion, nausea, gagging, the urge to vomit, and the desire to avoid contact with, and withdraw from, the eliciting stimulus[3,6,8]. These feelings have corresponding psychophysiological components, including decreased gastric activity[9,10]. Furthermore, across cultures, disgust is elicited by stimuli that would have reliably harboured pathogens in ancestral environments[1,11] or by objects that have been contaminated by touching those stimuli[7,8]. Such evidence, and the fit between disgust's form and its proposed function, has led to disgust being conceptualised as *the* pathogen and parasite avoidance emotion[2–5]. However, ectoparasites do not infect by being ingested or by a person merely touching contaminated matter; instead, they actively seek out a host, attach to the host's body surface, and feed on the host.

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Accordingly, nausea, appetite suppression, and behavioural sensitivities and motivations that reduce the risk of incorporation are not functionally suited to defend against ectoparasites. 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. We will refer collectively to these mechanisms as the ectoparasite defence system, distinguishing it from the pathogen avoidance system.

We recognize that some mechanisms of the ectoparasite defence system may serve other related functions; for example, in addition to being part of a mechanism to combat ectoparasites, itch may also be a response to botanical toxicants. Additionally, we recognize that ectoparasite and pathogen defence systems may not be completely dissociated. The systems address overlapping adaptive problems because similar types of organisms can threaten via ingestion or via infestation of the body surface: for example, arthropods can be agents of decay, disease vectors, and potential ectoparasites, so they may serve as an input to both systems. In addition, the behavioural outputs of pathogen disgust – withdrawal and avoidance – are useful, if partial, solutions for managing both types of threat. Moreover, unlike defensive responses to predators – fight, flight, or freeze[12] – the outputs of pathogen and ectoparasite defence are unlikely to interfere with each other's operation, leaving room for co-activation, or even entanglement, of their mechanisms. Nonetheless, we believe that the existing evidence indicates that the task demands, eliciting cues, and behavioural responses differ sufficiently between ectoparasite defence and pathogen avoidance as to merit describing these as two distinct systems. In the next section we review evidence indicating that selection pressures from ectoparasites have shaped specialised ectoparasite defence mechanisms in animals. As will be seen, ectoparasite defence adaptations are at least as phylogenetically ancient as pathogen avoidance mechanisms, appear to be conserved across phyla, and are likely to have homologues in humans.

2. Ectoparasite defence across species

Evidence from nonhuman animals demonstrates that selection pressures from ectoparasites are considerable, and, correspondingly, there is evidence that across diverse taxa, including insects, birds, and mammals, animals have adaptations for ectoparasite defence[13–15]. Consideration of the relevant selection pressures, and the form and function of these adaptations, can thus guide insights into the expected features of human ectoparasite defence mechanisms.

a) Ectoparasites as sources of selective pressures on animals

Ectoparasites exert demonstrable costs on host fitness. One investigation found that horses can lose up to half a litre of blood per day from fly bites[16], and studies have found that the presence of flies is associated with reduced weight gain[17] and milk production[18] in cattle. Ectoparasites such as ticks and lice can cause anaemia, as well as weight loss, which can even be fatal if parasite burdens are particularly high[19]. For example, half of all infant deaths in one study population of Chacma baboons are thought to have been due to ticks[20]. Direct fitness effects have been demonstrated by experimental manipulations showing that the presence of ectoparasites decreased the number of fledglings in barn swallows[21] and the survival rate and number of broods in cliff swallows[22,23]; the survival rate of ectoparasitised juvenile gerbils was half that of ectoparasite-free gerbils[24]; and experimental anti-ectoparasite treatment of female Cape ground squirrels quintupled the number of offspring produced[25]. Additional fitness costs can result from social avoidance when ectoparasites are detectable by conspecifics; for example, female pigeons avoid males who are infested with lice[26]. Importantly, primates must also constantly combat ectoparasites. For example, experiments with red-tailed guenon indicate that merely walking through the bush in the animal's natural habitat results in the acquisition of eight ticks per hour[27], and Japanese macaques typically harbour over 500 louse eggs at any one time – if not constantly suppressed through grooming, this number can increase 30-fold in a month[28]. In addition to the direct costs they inflict, many ectoparasites are also vectors for pathogens. For example, high death rates have been recorded among howler monkeys due to outbreaks of yellow fever spread by mosquitos[29] and among bonnet macaques due to arboviruses spread by ticks[30].

b) Behavioural adaptations for ectoparasite defence in animals

Selection pressures from ectoparasites are thought to have led to the evolution of ectoparasite defence behaviours[14]. Animals have specialized movements for repelling biting flies, including ear twitching, muscle twitching, tail swishing, and leg stamping[31], behaviours that are more frequent when fly density is high[32]. Other ectoparasites are less easily deterred, hence grooming and preening behaviour is present in numerous species, and is often one of the most time-consuming activities. For example, rats have been estimated to spend one third of their waking time grooming[33], and impala have been observed to orally groom and scratch over 1000 times per 12 hour period[34].

Grooming behaviours are costly: in addition to opportunity costs, grooming can be energetically expensive – experimental infestation of mouse-eared bats with mites caused elevated grooming, proportional to parasite load, that increased metabolic rate and weight loss[35]. Other costs of grooming include

diminished ability to detect predators and rivals[36,37], saliva depletion, tooth wear, and hair loss[38]. It is worth paying these costs because grooming is an effective anti-parasite behaviour. Impala that were allowed to groom reduced their tick load to one-twentieth that of impala prevented from grooming[39]. Mice prevented from orally grooming had 60 times the normal lice loads[40]. Cats that were able to orally groom reduced their population of fleas by half[41]. Chickens infested with lice were found to preen at 5-10 times the rate of non-infested chickens[42], and when debeaked chickens were seeded with lice, one month later they had over 20 times the number of lice as chickens with intact beaks[43].

c) Stimulus-response grooming and programmed grooming in animals

Evidence suggests that selection pressures from ectoparasites have led to the evolution of two broad forms of grooming in nonhuman animals, referred to as *stimulus-response grooming* and *programmed grooming*[38,44,45], or *scratch* and *scan* grooming[46]. Stimulus-response grooming involves immediate responses to cues to the presence of ectoparasites, such as the sensation of having been bitten, whereas programmed grooming involves periodic bouts of sequenced grooming movements that are thought to be endogenously generated, perhaps by an ultradian clock in the central nervous system[38]. Stimulus-driven grooming is a swift response to cutaneous sensations that cue the location of ectoparasites, eliciting a rapid grooming reaction directed at that location[38,47]. Cutaneous sensations include, for example, itching caused by histamine released following ectoparasite bites[14,48]. As discussed later, we suggest that 'tickling' sensations might be another cutaneous cue that elicits stimulus-response grooming, as these sensations may index the movement of ectoparasites on the body surface.

Extensive empirical evidence supports the existence of programmed grooming – grooming that occurs even in the absence of peripheral stimulation by ectoparasites. Animals in ectoparasite-free captive environments, such as zoological parks, still groom[38], as do wild animals like bighorn sheep living in a tick-free desert environment[49]. Stimulus-response grooming alone would not be an adequate defence because ectoparasites might frequently evade cutaneous-sensory mechanisms, and programmed grooming may be particularly effective at removing ectoparasites that are numerous or unlikely to activate cutaneous-sensory mechanisms, such as those in larval and nymphal stages, as well as adult ectoparasites before they have attached to feed[38].

The strength of the selection pressures shaping this adaptation is illustrated by the fact that, when comparing between species, or between juveniles and adults of the same species, smaller animals engage in more frequent programmed grooming than larger animals, reflecting the greater ratio of surface area to body mass in the former, and thus the proportionately larger vulnerability to ectoparasites[44,45,50]. In addition, as predicted by Mooring and colleagues, males in sexually dimorphic species trade-off ectoparasite defence against vigilance for oestrus females and rival males, and thus engage in less frequent programmed grooming[51,52]. The frequency and duration of programmed grooming bouts may be modulated by external stimuli that index increased vulnerability to ectoparasites, such as visual or tactile cues to their presence[14,39,48]. Programmed grooming can involve a complex sequence of movements, such as alternate teeth and tongue movements in ungulates[38], or, in mice, a stereotypical chain of head-to-toe (cephalo-caudal) movements of the front paws[47].

Consonant with fundamental functional differences between stimulus-response grooming and programmed grooming, in mice, these two classes of behaviour are controlled by partly distinct neural mechanisms, with the basal ganglia having a particularly important role in programmed grooming[53,54]. Notably, some evidence suggests that certain disorders in humans that involve excessive grooming behaviour, such as obsessive-compulsive disorder and trichotillomania (discussed below), also involve dysregulation of basal ganglia activity[55].

d) Ectoparasite defence behaviour in nonhuman primates

Primates groom by scratching, picking with their digits, or by using the mouth to remove ectoparasites[27,56]. Although these movements are similar to those shown to effectively defend against ectoparasites in other species, and primate researchers recognise that the original function of grooming was ectoparasite defence, some investigators argue that grooming came to have a primarily social function in primates[57,58]. Allogrooming, for example, may reinforce alliances and maintain social bonds [58–60]and even autogrooming, or self-directed behaviour, has been argued to have a primarily social function in alleviating stress during social encounters[61].

Although voluminous evidence supports the social importance of grooming in primates, the existence of such derived traits should not be taken as indicating that corresponding ancestral adaptations are no longer functional. On the contrary, there is good evidence that, consistent with other taxa, in primates grooming importantly defends against ectoparasite infestation. One recent study[62] found that variation in rates of autogrooming among Japanese macaques was better explained by lice loads than by social or environmental factors. Studies of many primate species show that autogrooming is confined to easily accessible regions of the individual's body, whereas allogrooming is focused on invisible and inaccessible regions such the head, neck,

and back[63–65] and within inaccessible regions, allogrooming is distributed evenly[63]. These patterns are consistent with behaviour designed for efficient ectoparasite removal, rather than merely social contact or communication. Furthermore, the form of grooming movements reflects an ectoparasite removal function: typically, primates stroke and visually inspect the fur, then pick up adult lice with the digits or mouth, or comb lice eggs along an individual hair using the nail of the first finger and the tip of the thumb, before ingesting the product[56]. Finally, grooming in primates has been shown to effectively reduce ectoparasite loads[56,66]. For example, yellow baboons that were groomed more by conspecifics had fewer ticks, fewer wounds attributed to clusters of feeding ticks, and less anaemia than those groomed less[67]. Thus, although grooming may have important social functions in primates, these appear to be built atop, rather than having replaced, the original ectoparasite defence function of grooming. Indeed, allogrooming might play such an important role in social exchange and bonding largely because it is valuable to the recipient as defence against ectoparasites[68].

Although research into primate grooming has not generally considered the distinction between stimulus-response grooming and programmed grooming, self-directed behaviours such as scratching are likely to be initiated by peripheral stimuli such as arthropod bites and itch[62], whereas bouts of extensive autogrooming seem unlikely to depend on peripheral stimuli, especially in the case of nit-picking behaviour. This could be confirmed using experiments similar to those conducted to investigate grooming behaviour among ungulates in ectoparasite-free environments[38,49]. Although allogrooming could still be interpreted as social in function in these circumstances, the persistence of autogrooming in ectoparasite-free environments would presumably reflect endogenously controlled programmed grooming. Anecdotal observations that grooming still occurs among primates in ectoparasite-free captive habitats has sometimes been interpreted as showing that grooming must have a social, rather than an ectoparasite-removal function[69]; however, these observations could also be explained as endogenous urges that are not dependent on peripheral stimulation by ectoparasites.

e) From animals to humans

Paralleling other host species, humans are likely to have been subject to extensive selection pressures stemming from arthropod ectoparasites such as mites, fleas, lice, ticks, bedbugs, and sand fleas. Phylogenetic continuity between primate and human ectoparasites is well documented in some cases, as genetic evidence shows that human lice and chimpanzee lice shared a common ancestor around 6 million years ago, at around the time that their hosts diverged[70]. Arthropod ectoparasites not only cause direct harm to humans by sucking blood, but, moreover, are important vectors of infectious diseases affecting our species: Lice spread typhus, trench fever, and relapsing fever[71]; ticks spread encephalitis, Lyme disease, and haemorrhagic fever[72]; scabies mites can cause streptococcal skin infections, renal disease, and rheumatic fever[73]; and fleas spread plague, typhus, and spotted fever[74]. Similarly, biting flies, such as mosquitos, black flies, and tsetse flies, both inflict direct costs through blood loss and are vectors for numerous diseases afflicting humans, including malaria, dengue, West Nile virus, chikungunya, yellow fever, and many forms of encephalitis[75]. Infestation can also have social costs; for example, people infested with lice[76–78] or scabies frequently report being the targets of exclusion and stigmatisation.

Given the highly plausible continuity throughout hominid evolution of selection pressures from ectoparasites, we should expect phylogenetic continuities between animal and human ectoparasite defence systems. Before examining human ectoparasite defence in detail, we begin by noting indications of such continuities. Although behaviours do not fossilise, archaeological evidence, including nits found on lice combs[79,80], indicates that grooming is an ancient practice, not merely a modern invention. We suggest that continuities between animal and human ectoparasite defence systems extend to the distinction between programmed and stimulus-response grooming: people clearly react to external cues associated with ectoparasites, experiencing feelings of skin crawling and itching, and scratch at the site of these sensations. This behaviour resembles the stimulus-response grooming described in animals, and its frequency will similarly depend on the frequency of cutaneous sensory experiences.

Although humans may not perform a stereotypical chain of grooming movements akin to those evident in mice[47], we suggest that, like non-human animals, humans have both stimulus-driven and programmed forms of grooming. Specifically, endogenous, programmed, grooming behaviours in humans plausibly include periodic inspection of the skin, and picking at, rubbing, or otherwise manipulating, the skin and hair – non-pathological behaviours that are performed daily by most people[81,82], and are likely homologous with primate grooming. We expect that research will show that, unlike stimulus-response grooming, these behaviours are not initiated by cues to ectoparasites (though they might be modulated by them), nor are they accompanied by motivational states or feelings, such as disgust, that are conceptually associated with ectoparasites. Rather, as endogenously generated behaviours, they will seem both spontaneous and inherently gratifying, and will frequently be performed absent-mindedly – indeed, they may often be enacted without extensive awareness, and may even go entirely unnoticed. Likewise, such behaviours

will often not be associated with self-presentation concerns and conformity to cultural expectations – on the contrary, they may even be proscribed (e.g., nose-picking), or may diminish, rather than enhance, appearance as measured by cultural standards. As we discuss below, these impulsive grooming behaviours might be the ordinary versions of excessive programmed grooming seen in trichotillomania and skin-picking disorders. In line with the animal literature on programmed grooming, the behaviours may be upregulated by cues to ectoparasite presence and down-regulated by trade-offs with competing motives such as mating effort.

We recognise that human grooming behaviour includes a large cultural component, as the practices whereby people clean their bodies vary widely from society to society, and are socially transmitted through teaching and learning (e.g.,[83]). Importantly, however, the cultural aspects of many human grooming practices should not lead to the conclusion that culture constitutes the totality of the phenomenon, as such practices are likely built atop biologically evolved ectoparasite defence mechanisms. For example, it appears that in many societies it is normative to engage in various prescribed self-grooming procedures prior to going to sleep. Although self-presentation concerns are a powerful determinant of conformity to cultural norms, pre-sleep grooming, especially when performed in private, is not readily explained in such terms. Rather, this pattern may reflect the institutionalization of an endogenous increase in autogrooming motivation in the evening (see discussion of circadian rhythms, below) – in short, programmed grooming may importantly underlie such cultural practices.

Viewing human grooming practices as a blend of cultural and endogenous factors generates the prediction that there will be similarities in grooming behaviour across cultures. Although some observations have been collected on grooming practices across cultures[84,85], we know of no equivalent work on endogenously motivated actions resembling programmed grooming. Indeed, in general, systematic research has been conducted on the forms that grooming takes in humans, especially outside of sanitised, relatively ectoparasite-free modern environments. This is not to say that behaviour of people from highly sanitised environments is uninformative. For example, to the extent that, as we suggest above, people in the developed world engage in spontaneous, endogenously motivated grooming behaviour, this parallels findings adduced in support of the existence of programmed grooming in nonhuman animals, such as the fact that sheep autogroom even in tick-free environments[49]. Nevertheless, the evolutionarily novel nature of hyper-clean environments is such that caution is in order when drawing inferences from behaviour observed in these settings. Studies of human grooming in societies suffering high ectoparasite loads are therefore sorely needed. Promisingly, one recent study documented grooming behaviours directed at ectoparasite removal, and hygiene behaviours such as washing and bathing, in six small-scale societies in which individuals have minimal or no access to modern medicine and public health[86]. In each of these societies, substantial time was devoted to grooming, equivalent to that expected for a primate of our body size and social group size[86]. However, this study did not distinguish between auto-grooming and allogrooming; while the latter serves parasite and pathogen defence goals, critically, it also addresses social-bonding functions[87] that are likely particularly important in face-to-face communities. Future research might therefore more precisely investigate the form and frequency of auto-grooming in general, and endogenously motivated grooming behaviours, in particular, in societies with differing parasite loads.

Despite the paucity of anthropological and naturalistic evidence regarding human grooming behaviour, recent studies in psychological disciplines have begun to shed light on human adaptations for defence against ectoparasites. However, before turning to active ectoparasite avoidance mechanisms, we first discuss one postulated gross morphological adaptation.

3. Human hairlessness and ectoparasites

Dating back more than a century, authors have suggested that human hairlessness might be an adaptation to diminish ectoparasite load by reducing the habitat in which ectoparasites can easily hide[88–90]. Pagel and Bodmer note that when humans are infested, ectoparasites are usually primarily confined to hairy regions such as the head and pubic area, perhaps because ectoparasites avoid hairless areas, or because hairless areas are more easily groomed and washed[89]. Of course, humans are not strictly hairless, having retained fine body-hairs rather that losing them altogether, and one account argues that fine hairs were themselves retained as ectoparasite-detection devices[91]. In support of this hypothesis, subjects more rapidly detected the presence of insects on fine-haired skin than on truly hairless shaved skin.

The selective advantage of hairlessness may have been accelerated by sexual selection if hairlessness was subsequently used as a cue to lower ectoparasite load. Several studies[92,93] have attempted to support the sexual selection account indirectly by showing that the contribution of body hair to attractiveness is influenced by pathogen prevalence, perceived vulnerability to disease, or disgust reactions to both cues of contaminants and cues of ectoparasites. The logic of these studies is that being hairless should be particularly attractive when pathogen or ectoparasite risk is elevated, especially among those who are most sensitive to disease threats.

While intriguing, it is difficult to test the importance of ectoparasite defence against other accounts of human hairlessness. Phylogenetic trends of primate hair density allometry combined with thermoregulatory efficiency[94,95] may suffice to explain hairlessness, and body-hair preferences can be explained as ephemeral fashions and fads, or responses to population-specific levels of hirsuteness, plausibly reflecting genetic drift.

4. The human ectoparasite defence system
a) Reactions to Ectoparasites

Turning from the morphological to the psychological, several studies have shown that insects and other arthropods evoke disgust[96,97], yet few studies have investigated whether the disgust reported by participants is characterised by prototypical disgust feelings of nausea and the urge to vomit, or, in contrast, involves feelings consistent with ectoparasite defence, including skin sensations such as itching. One recent exception is the work of Blake and colleagues[98], who compared participants' subjective-feeling responses towards vignettes describing dog faeces versus spiders, and towards videos showing vomiting versus spiders. Although there was overlap in the feelings described towards each type of stimulus, faeces and vomit primarily elicited prototypical disgust feelings, including nausea and the urge to vomit, whereas spiders primarily elicited feelings such as skin-crawling and the urge to scratch -components of a skin-focused affective experience. Blake et al., who do not draw a sharp distinction between skin contact as an avenue of pathogen transmission and skin responses to ectoparasites, term this experience "the heebee jeebies". While we applaud Blake and colleagues' pioneering work in this area, we avoid this term, as it derives from an American folk affect concept that may unhelpfully blur distinctions between skin-focused responses and what has been termed the experience of the uncanny[99]. Blake and colleagues also found that shivering, goosebumps, and chills were recalled more frequently by participants in response to ectoparasites and other skin-contact elicitors than in reaction to oral-gastric elicitors. They also noted that, in several languages, connotations of shivering, goosebumps, or chills accompany the term most readily translated as "disgust". We believe these sensations may reflect functional features of an ectoparasite avoidance system. Shivering, body-shaking, and head-shaking are common components of mammalian stimulus-response behaviour following ectoparasite detection[14,32], and may constitute understudied concomitants of human reactions to cues of ectoparasite risk. Likewise, "goosebumps," or, more properly, piloerection, can plausibly be understood as a response that enhances the host's ability to identify the location of mobile ectoparasites by placing hair shafts perpendicular to the organism's path of travel.

Other recent research found that when participants were exposed to maggots – intended as an experimental cue of the presence of pathogens – the tactile sensitivity of their skin (measured using monofilament force detection) increased[100]. These results raise additional questions, however, because maggots potentially constitute a multiplex stimulus – being associated with putrefaction, they can indeed index pathogen risk, but their resemblance to organisms such as larval ectoparasites, *Dermatobia hominis* (human botfly), or neosomous female *Tunga* (sand fleas)[101] is such that they potentially also cue ectoparasite risk. These studies did not compare the effects of unambiguously distinct ectoparasite cues and pathogen cues on upregulation of the skin's tactile sensitivity; a useful follow up study would therefore be to investigate whether tactile sensitivity increases more in response to ectoparasite cues than in response to pathogen cues.

At the level of behavioural response, several studies have found that human grooming behaviour increases in response to ectoparasite-relevant cues. Participants who were exposed to a presentation about parasites subsequently reported more urges to groom than those shown a presentation about the circulatory system[102]. Similarly, participants who watched videos of head lice or of people scratching reported more itching sensations and displayed more scratching behaviour than participants who had watched videos relating to cold or pain[103]. Another study found that participants shown images of arthropods such as fleas or ants reported more itchiness, and performed more scratching behaviour, than participants shown images of animals such as fish and birds, even if the arthropods were depicted crawling over the ground and not on human skin[104].

These studies show that stimulus-driven grooming increases when people see cues to the presence of ectoparasites, including merely pictures of ectoparasites. Whereas studies of nonhuman species are largely limited to measuring behaviour, and generally cannot explore subjective experience, investigations of humans reveal that grooming is often preceded by itch, or related sensations such as skin crawling. Furthermore, these sensations can be induced not only by histamine release at the site of parasite bites[14,48], but also simply by exposure to images of ectoparasites[104]. Some investigators have suggested that images of ectoparasites trigger itching due to classical conditioning among people who have previously been bitten by the ectoparasites depicted[105]. However, it has not been shown that previous biting is necessary for these effects, and it is possible that merely appraising stimuli as cues to the presence of ectoparasites is sufficient to trigger the response. One limitation of these human findings is that none have compared the effects of disgusting pathogen cues with the effects of ectoparasite cues on the degree of skin sensation and frequency of grooming

movements, so, at present, it cannot be concluded with certainty that the observed itching and grooming responses are indeed distinct from pathogen disgust.

b) **Reactions to social cues of ectoparasites**

Studies on contagious itch have shown that viewing images or videos of other people scratching increases participants' itching sensations and scratching movements[104,106,107]. In fMRI studies with human subjects, observing scratching videos elicited contagious itch and scratching behaviour, with the same brain regions of the 'itch matrix' being activated as occurs with itch induced by histamine application, including the anterior insula, premotor cortex, primary somatosensory cortex, and prefrontal cortex[108]. The right anterior insula was activated most consistently; this region serves interoceptive states including itch, tickle, and visceral pain[108]. Partly based on findings such as these, several authors have suggested that activation of the mirror neuron system is responsible for contagious itch[106,108,109]. However this suggestion is difficult to reconcile with findings, in both humans and macaques, that the body part scratched by the subject is usually different from the area scratched by the individual observed, and observers also often use a different hand from the target[110,111]. This is unusual for contagious experiences: in vicarious experiences of pain[112] or touch[113], the location of vicarious experience corresponds to the body part observed. Relatedly, whereas mirror neuron reactivity is positively correlated with empathic concern as a personality trait[114], contagious itch reactivity shows no such association, instead being positively correlated with trait neuroticism – a connection that may be based on sensitivity to hazards[108].

One possible explanation is that if, as we suggest here, the main function of itch is ectoparasite defence, then the itch response should be potentiated by cues to the presence of ectoparasites. The sight of arthropods (real or recorded) serves as a cue to the presence of ectoparasites, leading to increased skin sensitivity and potentiated itch – and observing conspecifics scratching likely has similar cue value. If conspecific scratching is a general cue to the presence of ectoparasites, then global skin sensitivity should increase, along with increased vigilance to skin sensations and decreased itch threshold. The location of a contagious itch might therefore be the result of cutaneous stimulation that would not normally pass the threshold required to generate itch and corresponding scratching behaviour. Of course, not all cues are equally informative: because a given conspecific may scratch for a variety of reasons that are independent of the presence of ectoparasites (e.g., anxiety[61]), observing a conspecific scratching is a less reliable index of ectoparasite presence than observing ectoparasites directly; correspondingly viewing images of insects induces more intense itch than does viewing others' scratching behaviour[104].

c) **Key unanswered questions regarding human ectoparasite defence systems**

Evidence has thus begun to show that humans respond to stimuli that cue ectoparasite risk with sensations, such as itching, and behaviour, such as scratching, that are functionally consistent with ectoparasite defence. As such, these results indicate that the human response to ectoparasite cues appears similar to the stimulus-response grooming seen in nonhuman animals[38,44]. However, many questions remain about human ectoparasite defence. For example, do different types of skin sensation arise from particular stimuli, and do these sensations prompt specific grooming behaviours? Tickling sensations might cue unattached ectoparasites landing or moving over the body surface, whereas itching might index attached or feeding ectoparasites. Correspondingly, tickling sensations might prompt brushing-off or wiping behaviours that function to dislodge unattached ectoparasites, whereas itching might stimulate scratching or picking behaviours that would more effectively remove feeding ectoparasites. Using the digits to pick at suspected ectoparasites might be a particularly effective behaviour when their location can be identified by visual inspection of the body surface.

Paralleling outstanding questions concerning human stimulus-response grooming, it will be critically important to identify the endogenous mechanisms controlling human programmed grooming, and to better understand the forms that programmed grooming takes in humans, especially outside of sanitised, relatively ectoparasite-free modern environments. Knowledge about human endogenous programmed grooming will be especially important if, as we propose below, whereas some clinical conditions are pathologies of stimulus-response grooming, others are likely explicable as pathologies of programmed grooming.

Human stimulus-response grooming and human programmed grooming may each exhibit adaptive circadian patterning revealing the precision with which relevant adaptations have been attuned to cost/benefit trade-offs in ectoparasite avoidance. It is notable that, in a number of diurnal primate species, autogrooming behaviour increases in the evening, prior to sleep[115,116]. Presumably, this is a time when the opportunity costs of programmed grooming are relatively low, providing a chance to remove some of the ectoparasites acquired during the day's travels. Complementing this is the importance of reducing the presence of ectoparasites prior to sleep, as sleep's combination of diminished awareness and reduced movement likely enhances the host's vulnerability to ectoparasites' depredations. Indeed, the common bed bug appears to have evolved to specialize in exploiting this vulnerability, as it becomes active at night[117]. Once asleep, the host's behavioural defences against ectoparasites must rely exclusively on tactile detection

and subsequent stimulus-response grooming. It may therefore be significant that there is extensive evidence in humans that itch sensitivity increases during sleep[118,119] suggesting an adaptive upregulation of this front-line warning system during periods of reduced awareness. In contrast to sleep, while awake, host defences can integrate itch modulation with other sensory modalities to maximize the cost/benefit ratio of attending to tactile sensations.

As illustrated by itch sensations and scratching behaviour, the features of human ectoparasite defence contrast with sensations such as nausea, and behaviour such as oral rejection, that are functionally consistent with pathogen avoidance. Nevertheless, an important topic to be investigated concerns the extent to which ectoparasite defence systems and pathogen avoidance systems overlap. One avenue for exploring this would be to examine the respective elicitors. Some cues might exclusively activate one system and not the other. For example, the smell of rotten meat presumably activates a gastric disgust response much more than a cutaneous ectoparasite defence response. Conversely, the sight of an ectoparasite, such as a flea or louse, may elicit both skin sensations such as crawling and itching and a feeling of revulsion and the desire to withdraw. What is unclear is whether the feeling of revulsion is a product of an ectoparasite defence mechanism, or of co-activation of a pathogen disgust mechanism, or whether ectoparasite defence mechanisms are facultative components of a more general pathogen and parasite disgust response. In this regard, it is important to note that self-reports of disgust towards both pathogen cues and ectoparasite cues do not by themselves constitute evidence that both types of stimulus elicit the same emotion, or even the same feeling, because the folk-affect term disgust is used by participants to refer to more than one distinct affective state[120,121]. For this reason, studies should aim to investigate affective responses and somatic sensations at a more fine-grained level. A related question is the extent to which facial expressions elicited by pathogens versus ectoparasites are the same; one reason to suspect differences is that the disgust expression's movements, involving constriction of the mouth, nose, and eyes, are thought to be adaptations to reduce infection by air-borne pathogens[122], but these movements seem less likely to offer protection from ectoparasites.

Future investigations into self-report, physiological reactions, and neural responses to various cues may help to clarify the degree of separation between the systems. Table 1 summarises the differences between ectoparasite defence systems and pathogen avoidance systems. In particular, we draw investigators' attention to plausibly functionally distinct features of reaction patterns, such as the distinction between, on the one hand, oral rejection, cleansing behaviours, and associated responses to cues of pathogen presence, and, on the other hand, shaking, scratching, and picking responses to cues of ectoparasite presence. Likewise, investigators might leverage the extensive corpus of work on ectoparasite defence in nonhuman animals to make predictions about ectoparasite defence in humans.

INSERT TABLE 1 ABOUT HERE

5. Clinical implications

Psychopathologies are often explicable as normally adaptive mechanisms that have gone awry[123,124]. Several authors have noted that the emotion disgust may play an important role in a number of clinical conditions, including contamination-related obsessive-compulsive disorder (OCD), eating disorders, some phobias, and impulse control disorders such as trichotillomania[125–127]. However, although some of these conditions, such as contamination-related OCD and eating disorders, may be straightforwardly related to pathogen disgust along with its primarily oral-gastric function, others may instead be more closely related to ectoparasite defence mechanisms. We also suggest that an important distinction can be made between conditions involving excessive programmed grooming that occur in the absence of ectoparasite detection, and stimulus-response conditions that may arise from disordered ectoparasite detection.

a) Disorders of programmed grooming

Compulsive skin picking and related skin damaging syndromes. The most common compulsive skin picking syndrome is trichotillomania, compulsive hair pulling, which may also include trichophagia – biting or eating the hair that has been pulled out[128]. Similar syndromes include 'trichotemnomania', obsessive cutting or shaving of the hair[129], 'trichoteiromania', repeated rubbing of the hair that can lead to hair loss[130], 'trichodaganomania', biting of the hair[131], rhinotillexomania, repetitive nose-picking[132], and onychophagia, compulsive nail biting[133]. The features of trichotillomania and skin-picking disorders appear consistent across cultures[134]. Most individuals report tension or nervousness before picking and while attempting to resist picking, but pleasure or relief after picking[135]. Thus skin picking and other grooming related syndromes need not be induced by cues to ectoparasite presence, but may instead be used to manage other sources of stress, yet still retain attributes, such as the oral component discussed above, or the concentration of behaviour in the pre-sleep period[136] that are adaptive in the context of ordinary ectoparasite defence.

Consistent with the suggestion that these conditions may be more closely related to ectoparasite defence than to pathogen avoidance, several psychodermatologists have suggested that disordered skin-picking and related syndromes may be continuous with normal human autogrooming, and may be

phylogenetically related to grooming in other mammals[137,138]. Non-pathological grooming behaviour in both humans and nonhuman animals becomes more repetitive under stress, indicating that skin picking and related syndromes might be exaggerated versions of normal grooming behaviour[61,137]. Moreover, similar pathological grooming conditions occur in nonhuman animals, including acral-lick dermatitis in dogs, psychogenic feather picking in birds, and psychogenic alopecia in cats[139,140]; indeed, the role of biting in trichophagia and onychophagia underscores possible phylogenetic continuities, as, in nonhuman primates, ectoparasites are often destroyed through biting, and are sometimes ingested[56].

It may be possible to explain the pervasive association – evident across a huge variety of species – between grooming, pathologies thereof, and stress, as a side-effect of functional features selected for by the fitness costs imposed by ectoparasites. Allogrooming is potentially considerably more efficient than autogrooming, as, unlike the solitary autogrooming individual, a grooming partner can readily reach all areas of the recipient's body[141] and can use visual inspection in all areas. In many social species, proximity and contact are fraught with the possibility of aggression, hence, ceteris paribus, propinquity can often be stressful. However, efficient allogrooming requires that the recipient remain relatively still to facilitate groomer visual and mechanical access, including the groomer's potentially rapid reactions aimed at countering mobile ectoparasites' defensive responses to grooming. The fitness benefits of receiving efficient ectoparasite removal at the hands (or mouth) of another may have selected for a suite of calming, rewarding responses that reduce vigilance and agonistic reactions toward conspecifics, both in service of remaining still, and in the service of promoting the receipt of valuable allogrooming[142–144]. These reactions both reflect, and set the stage for, affiliative interactions with conspecifics, facilitating mutually beneficial grooming exchanges, and, eventually, potentially playing a key role in the evolution of advanced sociality[60]. However, once in place, this suite of calming responses can also be employed for purposes unrelated to ectoparasite defence, being used instead for self-regulation – as evident in the association between anxiety and quotidian self-directed behaviour. At the extreme, this opens the door to the possibility of pathologies of grooming in the service of calming and anxiety reduction, as discussed above.

Other conditions (some of which are described below) can also involve repetitive skin picking behaviour, but are not classified as skin-picking syndromes if the behaviour is clearly secondary to pathological cutaneous sensations or psychotic symptoms such as delusions or hallucinations[137].

b) **Disorders of ectoparasite detection and stimulus-response grooming**

Entomophobia. Like many of the conditions discussed here, entomophobia, the fear of insects, spans a spectrum from commonly encountered mild forms to debilitating clinical manifestations[145]. While fears directed toward insects such as bees and wasps clearly centre on the possibility of harm independent of issues of parasitism, others, such as aversive responses directed at fleas, ticks, and leeches, are more clearly aimed at ectoparasite avoidance. Aversion to organisms, such as cockroaches, grasshoppers, and slugs, that do not parasitise humans, may be overgeneralizations of reactions towards ectoparasites. To date, for most target species, there has been little research concerning these reactions or their pathologically extreme versions. One notable exception is arachnophobia, the fear of spiders, one of the most prevalent animal phobias in contemporary developed societies[146]. Arachnophobia is often explained in terms of the selective pressure exercised on ancestral human populations by venomous spiders[147]. Without questioning the cogency of this account, we note that it is likely incomplete, as it does not fully explain the emotional tenor of the reaction. Specifically, studies have documented that arachnophobia involves not only fear, but also disgust[148]. However, as discussed previously, to date, most research on disgust has not clearly differentiated between reactions, such as nausea and desires for cleansing, that are functional in the context of pathogen avoidance, and experiences of skin-crawling, shivers, shaking, and piloerection, that fit better with ectoparasite defence. Accordingly, we suggest that more careful parsing of the disgust component of arachnophobia will reveal that this syndrome is at least partially explicable in terms of exaggerated ectoparasite defence. Indeed, the one existing investigation that has explored the differences in eliciting stimuli and qualia between reactions to events involving the skin and those involving other avenues of contamination, that of Blake and colleagues[98], found that, in recalled events, spiders, like lice, mites, and ticks, primarily elicited skin-sensations such as itching and crawling. For these reasons, we are as yet unconvinced by claims that spiders have special evocative potency relative to other arthropods due to a history of selection for avoidance of venomous spiders[149], as the comparison arthropods used have been innocuous rather than those that are (or resemble) parasites[149].

Trypophobia. This recently described condition[150]is an aversion towards clusters of roughly circular shapes, such as the holes on a sponge or clusters of bubbles in a cup of coffee. Being confronted with these stimuli can cause high levels of anxiety and distress[151]. In addition to aversions towards harmless clusters such as bubbles, individuals with trypophobia typically report strong aversion to clusters resembling parasites and infectious disease, such as a cluster of ticks[152], suggesting that the condition might be an overgeneralised response to cues to the presence of ectoparasites and infectious disease[152]. Recent research

showed that, in contrast to most phobias - which predominantly involve fear - the aversion towards clusters predominantly involves disgust[152]. Moreover, although many individuals described prototypical disgust feelings such as nausea, the most commonly described feelings were skin sensations including itching, crawling, and the feeling as if 'bugs' are on the skin[152], similar to the subjective responses of Blake and colleagues'[98] non-clinical subjects exposed to cues of ectoparasites. Although these sensations resemble those of delusional parasitosis, individuals with trypophobia do not believe that they are infested, but rather feel *as if* they are infested when they encounter cluster patterns. Thus, trypophobia appears to involve both prototypical disgust as well as cutaneous sensations consistent with ectoparasite avoidance, but, at present, it is not known whether these responses are coactivated, differ between individuals, or differ between cluster stimuli with different visual features.

Delusional parasitosis. People with this condition, also known as Ekbom syndrome or delusional infestation, believe that they are infested by ectoparasites despite medical evidence to the contrary. In most cases they also experience skin sensations such as itching and crawling, and even biting or stinging, which they believe to be caused by their ectoparasites[153,154]. Patients typically report being infested either with generic insects ("bugs"), or with a more specific ectoparasite such as scabies, lice, or fleas. Delusional infestation often impels patients to frequently clean their home, clothes, and body, and may also lead them to remove head and body hair, and to secondary conditions such as trichotillomania[155] and skin picking[156]. In a variant of delusional parasitosis termed Morgellons disease, patients believe themselves to be infested by threads or fibres[157]. The increasing frequency of Morgellons[157] may in part arise because individuals with delusional parasitosis disbelieve medical professionals who tell them that they have no somatic medical condition, and are therefore open to alternative scientifically-incredible, but, to them, plausible-sounding, explanations that are widely disseminated via the Internet.

c) Summary

We suggest that the conditions discussed above are disordered forms of normally adaptive ectoparasite defence behaviour. In particular, compulsive skin picking, and related skin-damaging syndromes may involve a disordered level of endogenous grooming, whereas delusional parasitosis and trypophobia may be disorders of ectoparasite detection mechanisms. Importantly, all of these conditions are likely to be separate from obsessive–compulsive disorder, which, in contamination-OCD, primarily revolves around concerns about pathogenic microorganisms. OCD involves intrusive thoughts and obsessions about threats, which may lead to compulsive behaviours that are repeated because they do not provide relief. In contrast, in skin-picking and related disorders, a general tension (rather than an intrusive thought) is experienced before picking, and gratification and relief are experienced after picking[135,158]. Notably, comorbidity between skin picking and OCD is infrequent[158,159], and comorbidity is also rare between OCD and delusory parasitosis[160] and between OCD and trypophobia[151]. OCD is unlike delusional parasitosis, because it involves obsessive fears about contamination, rather than an unshakeable belief in being infested by ectoparasites[161]. Likewise, OCD is unlike trypophobia, which is a reaction to external stimuli, rather than to internally generated thoughts. Hence, pathologies of pathogen avoidance and pathologies of ectoparasite defence appear to dissociate, as would be expected if they are largely distinct systems.

We also suggest that there is an important distinction between stimulus-response conditions, such as delusory parasitosis and trypophobia, and conditions involving excessive grooming, such as skin picking and trichotillomania. Grooming disorders appear to arise from endogenous impulses, rather than in response to external cues to the presence of ectoparasites. As such, these conditions are reminiscent of excessive versions of programmed grooming, and, similar to programmed grooming in nonhuman animals[44,48,162], the frequency of picking in grooming disorders increases in response to a variety of stressors, not merely in response to ectoparasite cues[137]. As noted above, if selection has favoured experiencing the receipt of grooming as rewarding and relaxing, then it makes sense that it could come to be a response to a variety of stressors and a favoured tension-reducing habit of anxious people. In contrast, delusory parasitosis and trypophobia do not arise from endogenous grooming impulses, but rather are responses to external (imagined or overgeneralised) ectoparasite cues. These conditions are more reminiscent of stimulus-response grooming seen in human and nonhuman animals. Progress in understanding all the above conditions may be aided by insights from research into human and nonhuman ectoparasite avoidance behaviours.

6. Conclusion

Much progress has been made in recent years by researchers seeking to understand human pathogen avoidance adaptations, especially relating to the emotion disgust. Here, we have proposed that research should also investigate human ectoparasite defence adaptations. Research into pathogen disgust has shown that it has important social and clinical consequences, contributing to prejudice, and playing a role in psychological disorders such as obsessive-compulsive disorder. Human ectoparasite defence psychology is also likely to have important clinical, and perhaps social, implications. Recognizing the distinct task demands and differing selection pressures of avoiding pathogens and defending against ectoparasites raises many

intriguing research questions, potentially illuminates a number of clinically important phenomena, and affords consilience between human affective science and nonhuman behavioural ecology. It is time for the scientific community to scratch this particular itch.

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Tables

Table 1. Summary of the differences between the pathogen avoidance and ectoparasite defence systems, especially as regards humans.

	Pathogen avoidance system	Ectoparasite avoidance system
Threat cue	Ingestible matter, olfactory, visual, and tactile cues associated with putrefaction	Macroscopic invertebrates, associated patterns (clusters; rashes) and behaviours (conspecific scratching behaviours)
Predominant subjective feelings	Nausea, revulsion	Cutaneous sensations (e.g. itching, skin crawling, tickling sensation*)
Characteristic physiological responses	Decreased gastric activity	Skin sensitisation*
Neural mechanisms	Insular, basal ganglia	The 'itch matrix' including anterior insula, premotor cortex*, primary somatosensory cortex, and prefrontal cortex. And, for programmed grooming, the basal ganglia
Behavioural outputs	Reduced feeding, withdrawal	Grooming (scratching, picking and brushing-off* movements)

*denotes hypothesised difference