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Review

Mate preferences and infectious disease: theoretical considerations and evidence in humans

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Mate preferences may operate in part to mitigate the threats posed by infectious disease. In this paper, we outline various ways in which preferring healthy mates can offer direct benefits in terms of pathogen avoidance and indirect benefits in terms of heritable immunity to offspring, as well as the costs that may constrain mate preferences for health. We then pay special attention to empirical work on mate preferences in humans given the depth and breadth of research on human mating. We review this literature and comment on the degree to which human mate preferences may reflect preferences for health.

Keywords: mate preferences; mate choice; disease avoidance; major histocompatibility complex; disgust

1. INTRODUCTION

Infectious disease is typically spread through biological vectors: other organisms that act as hosts for infectious agents include viruses, bacteria, fungi and macroparasites. Infectious disease is commonly acquired from individuals of the same species. Infections can spread from conspecifics via direct contact with an infected individual, contact with an individual's bodily fluids, air or other substances excreted or expired, or contact with food, water or other matter contaminated with those excretions. Opportunities for transmission through these forms of contact are pronounced for particular kinds of inter-individual relations. Mating relations are certainly among these, particularly in species in which sexual mates have prolonged periods of close contact. Animals should often be expected, then, to possess adaptations that function to avoid disease through preferential mating.

In this paper, we explore these adaptations. The paper has two primary sections. First, we discuss theory pertinent to mate preferences for health. Although preferences for healthy mates may function to avoid disease, they can have other functions too, which are relevant to discussing evidence pertaining to the functions of mate preferences. Mate preference has costs as well as benefits, and we identify some of the major costs of preferences that function to avoid disease. In this section, we also discuss models of preferences for disease avoidance in the literature and, relatedly, we attempt to identify the circumstances

and life histories of organisms particularly likely to evolve important mate preferences that function for disease avoidance. Second, we discuss literature pertaining to mate preferences for disease avoidance in one species: humans.

2. THEORETICAL CONSIDERATIONS

We begin with a consideration of factors that should, based on a theoretical analysis, affect mate preferences for healthy individuals and, more specifically, function for infectious disease avoidance. The strength and nature of mate preferences should depend on their net benefits, a function of their gross benefits and associated costs. Below, we discuss some of the major benefits and costs of preferences for mate healthiness.

(a) *What is health?*

Before addressing benefits and costs of mate healthiness, however, we briefly define what a 'healthy' mate is for the purposes of this paper. There are multiple facets to health as the term is used in the literature. Different forms of a mate's health offer different kinds of benefits to mate choosers.

(i) *Being minimally infected by harmful pathogens*

Absence of fitness-reducing infectious agents, including harmful bacteria, viruses, fungi, and protozoan and metazoan parasites is one facet of health. Some of these infectious agents can be transmitted directly to conspecifics, whereas others may not be. In the context of mate choice, it is important to distinguish this narrowly defined form of health from others precisely because of the potential for transmission to conspecifics, including mates. Given that the focus of this special

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issue concerns behavioural disease avoidance, we pay special attention to this particular facet of health. Nonetheless, an understanding of the evolution of preferences for mates who are free of infectious disease must be complimented by other aspects of mate health.

(ii) *Good condition*

A much more expansive concept of health effectively equates it with condition. Condition is broadly construed as an individual's ability to perform fitness-enhancing physiological processes, partly reflective of the robustness and efficiency of those physiological processes [1]. Empirical measurement of condition, broadly construed in this manner, is difficult; instead, condition is often measured more narrowly as the ability to assimilate energetic resources (e.g. growth rate, energy stores), for example as affected by ability to capture energetic resources from the environment (caloric production). Indeed, researchers often define condition more narrowly in this way [2–4]. When conceived broadly, condition may be compromised by a wide variety of recognizable diseases and injuries, including current infection, metabolic disease (e.g. diabetes), disease of an organ system (e.g. cancer, liver disease, atherosclerosis, schizophrenia), various genetic diseases, injuries (e.g. broken limbs) and downstream effects of a past pathogenic attack (e.g. rheumatic fever). Naturally, these categories are not mutually exclusive (e.g. a disease of an organ system may also be owing to mutations or past pathogenic attack). Variation in condition may also, however, reflect what are commonly recognized as 'normal' variations, such as variations owing to developmental robustness, as reflective of a history of perturbations in development (developmental instability; [5]), variations in metabolic efficiency, as affected by rate of production of oxidants during cellular respiration (e.g. owing to accumulations of toxins or mutations; [6]) and variations in dietary quality (e.g. vitamin deficiencies).

(iii) *Immunocompetence and other capacities to resist disease (health-proneness)*

Some capacities related to health do not reflect current condition as defined above, but rather are dispositional qualities indicative of future disease resistance. One such capacity is immunocompetence, itself reflective of two abilities: the ability of an individual's immune system to recognize pathogens (immune recognition) and the ability of an individual to mount an effective response to a pathogen once it has been recognized (immune responsiveness; [1]). Low rates of oxidative stress may constitute another such capacity, as oxidative damage may accumulate to affect disease in the future, in ways distinct from current health [6]. Because these capacities do not constitute aspects of current condition *per se*, it is perhaps most appropriate to refer to them as reflecting *health-proneness* rather than *health* or *condition*. Qualities affecting health-proneness, as opposed to current health, have received much attention in the mate preference literature [7].

One might expect current health (defined either narrowly as being free of infectious disease or broadly in terms of condition) to covary positively with health-proneness. After all, an individual who is healthy at one time may be expected to possess the capacities to maintain health in the future. Although current health and health-proneness may be expected to covary positively in many instances, they may conceivably independently vary or even negatively covary. The latter can occur when individuals in best condition have been selected to allocate their resources heavily into mating effort—intrasexual competitive abilities, attractive displays and risk-taking—to such an extent that they allocate fewer resources into functions that maintain longevity and future health, such as immune responsiveness and antioxidants [3,8,9]. Indeed, under such circumstances of heavy investment in mating effort, individuals who are most fit may actually be more likely to currently carry an infectious disease [8].

(b) *Benefits of preferring healthy mates*

Preferring healthy individuals as mates (e.g. avoiding infected individuals as mates, avoiding individuals that are disease-prone as mates) could, in theory, yield at least three distinct categories of reproductive benefits.

(i) *Direct benefits in the currency of infectious disease avoidance*

Close physical contact with a conspecific that carries an infectious disease entails a risk of transmission of the pathogen to self, regardless of that contact being sexual or non-sexual. Preferences for healthy mates, then, benefit an individual by reducing the chance of acquiring an infectious disease [10–13]. If mating takes place over a discrete, short time course, then *current* disease status is of sole importance in this regard. In instances of biparental care, in which partners are in close proximity for a mating season or multiple years, one can also benefit from choosing a mate that is not prone to infection, so future infection risk is limited. In such instances, direct benefits via disease avoidance could, in theory, be obtained through preferences for individuals with cues or signals of immunocompetence, independent of current infection.

Again, close interaction partners of all sorts could potentially transmit a disease to self. Sexual contact typically involves the especially close contact required for gamete transmission. Additionally, bodily fluids that are rarely exchanged during non-sexual interactions may be encountered during sexual interaction; these fluids may transmit pathogens. Further, when sexual contact is involved, specifically sexually transmitted diseases (STDs) can be transmitted. Because STDs are transmitted primarily through sexual contact, special considerations apply to them, as we discuss below.

Again, the specific benefit of disease avoidance is of particular interest to the current article and issue. To appreciate the circumstances under which preferences for infectious disease-free mates will evolve, however, other benefits and costs must also be considered.

(ii) *Direct benefits in the currency in the net value of care for offspring*

At instances in which one sex (typically females) exerts parental investment, the other sex benefits from choosing a mate that is able to care for offspring. To the

extent that disease compromises the ability to deliver care to offspring (either in terms of quality of care or longevity of care), individuals of the less investing sex disproportionately benefit from choosing a healthy mate. For example, in species in which females (but not males) provide investment in offspring, males (but not females) may benefit from selecting a mate less likely to lose investment ability owing to infectious disease. Naturally, in instances of biparental care, both sexes benefit from choosing a mate able who is to care for offspring and, hence, healthy.

Additionally, diseased individuals may transmit the pathogen to offspring during care (whether during gestation or postnatal care), further reducing the value of their care to a mate chooser. The latter benefit does not exist, of course, when the disease is transmittable only through sexual contact. We note, however, that some STDs, such as (in humans) human immunodeficiency virus (HIV), can be transmitted to an offspring via nursing, and many other, such as (again, in humans) *Chlamydia* and herpes simplex I, can be transmitted during gestation or birth.

Finally, parents may transfer (e.g. *in utero*, through lactation) antibodies to pathogens, thereby enhancing the health-proneness of offspring. An immunocompetent individual may accordingly offer benefits to a mate via this process.

(iii) *Indirect benefits boosting offspring fitness if health or health-proneness is heritable and associated with fitness*

Mate choosers can benefit from mating with an individual possessing genes that boost offspring fitness, either because the genes are intrinsically good (good independent of the qualities or genotype of the mate chooser) or compatible (specifically good for the mate chooser, in the light of her or his genetic make-up). If both health or health-proneness is heritable and associated with fitness, then, for this reason, it can pay to choose mates that are healthy or that possess cues or signals of health-proneness.

We note that it is not sufficient for immunocompetence to be heritable for mate choosers to gain net indirect benefits for offspring by selecting healthy mates. At a stable equilibrium, fitness may positively covary, negatively covary or be uncorrelated with current health or immunocompetence [8,9,14–16]. More generally, viability and longevity need not positively covary with fitness or heritable fitness. As noted above, in systems characterized by extreme sexual selection (e.g. winner-takes-all competitions), the few males of sufficient condition or fitness to currently place themselves in the fray of competition (whether through costly signalling or direct intrasexual competition) may benefit from investing energy in mating effort to the detriment of health. Despite their superior fitness, these males possess lower viability (including immediate and long-term health) than less fit males that, in a sense, 'stood on the sidelines' and never entered the competition (at least during the current bout). The ultimate subset of winners of the mating competition may also possess, on average, higher levels of morbidity and lower levels of longevity than the average male in the population [8].

(c) *Costs of preferences for healthy mates*

We now turn to the cost side of the equation. What are the potential costs of preferences for healthy mates?

(i) *Search costs*

Any mate preference carries with it potential search costs [7]. Mate preferences, if at all meaningful, entail a non-zero rejection rate. If the encounter rate with members of the other sex is sufficiently low, then these costs could be considerable.

In mating systems in which only one sex is choosy, search costs for that sex are driven by its level of choosiness and its encounter rate with members of the other sex. In mating systems in which mutual mate choice exists (i.e. both sexes are choosy), search costs vary as a function of an individual's level of choosiness and the encounter rate with members of the other sex that will accept self as a mate. Naturally, the former factor can affect the latter. For example, if the increasingly small subset of mates that one finds acceptable as choosiness increases also become more choosy themselves, as is expected if individuals with valued features can afford to be choosier, the risks of not finding a suitable mate increase. In such instances, the costs of choosiness for health accelerate as choosiness increases.

(ii) *Opportunity costs*

Relatedly, in a sex that can conceive offspring iteratively (e.g. males that exert zero-parenting effort), non-zero rejection rates entailed by mate preference have opportunity costs: rejection of potential sex partners could result in loss of potential reproductive events. For choosiness based on health to evolve, the benefits of being choosy (e.g. as affected by disease avoidance) must exceed the net costs of foregoing those potential reproductive events.

(iii) *Trade-offs with other preferences*

A preference for healthy mates can have costs associated with trade-offs with other valued features for at least two distinct reasons.

Because healthiness may negatively covary with other valued features, preferences for mate healthiness, in the absence of other preferences, may lead to mating with individuals that, on average, are inferior with respect to other valued traits. As discussed above, for instance, species in which sexual selection on males is extreme, males with greater fitness (and those with greater heritable fitness) may, on average, have lower viability and greater levels of morbidity. Hence, preferences for health in such instances could actually lead to mating with individuals offering lower indirect genetic benefits to offspring [8,9].

Special considerations may apply to STDs. Even in species in which males with greater heritable fitness possess, on average, greater health and longevity, they may nonetheless carry STDs at greater rates, for the obvious reason that they have more opportunities to become infected with STDs [17–19]. In these instances, mate preferences based on avoiding STDs could, once again, lead to mating with individuals offering fewer indirect genetic benefits to offspring. If males provide direct benefits of protection for offspring, it is similarly possible

that males offering the best protection actually carry STDs at greater rates. At the same time, selection on sexually transmitted pathogens themselves may favour them to be cryptic and, hence, preferences for cues of being infected by STDs may be lacking (see [20]; see further discussion below).

Second, if search and opportunity costs are to be kept constant (e.g. choosiness is constant), then preferences for healthy mates obviously constrain preferences for other valued features, even if those features positively covary with healthiness. One might argue that this cost is not independent of search or opportunity costs, already discussed. This may be the case if search or opportunity costs increase additively with choosiness and valued features are uncorrelated: a preference for healthiness increases a constant amount of search or opportunity cost, independently of search or opportunity costs incurred by choosiness on other dimensions. As noted above, however, in instances of mutual mate choice, choosiness may entail costs that accumulate non-additively. In such instances, costs of preference for healthy mates are not independent of preferences for other features. The more one values other features (i.e. the choosier one is, independently of choosiness for health), the greater the cost one pays for being choosy about health. Hence, for any given level of search or opportunity costs for preferring healthy mates, one does face trade-offs with other preferences.

(d) Models of mate preference for health and disease avoidance

The special focus of this article is preference for mates who are free of infectious disease for the function of behavioural disease avoidance. In light of the costs and benefits of preferences for healthy or health-prone mates, under what conditions are these preferences expected to evolve?

Perhaps somewhat surprisingly, evolutionary biologists have performed little modelling of these preferences. Any complete understanding of the evolution of preferences for health or health-proneness is likely to require a consideration of a variety benefits, including indirect benefits, which may or may not, once again, positively covary with current disease status [1,7,21]. Modelling to date has only examined the evolution of preferences for being disease-free in very simplified mating systems [13,17–19].

Though doing so in the absence of an explicit cost–benefit model carries risks, we nonetheless explore answers to the question posed above: under what circumstances can preferences for mates who are disease-free for the function of disease avoidance be expected to be relatively strong? By contrast, under what circumstances can they be expected to be weak?

(i) When benefits to disease avoidance are relatively great
Some species evolve to benefit from a slow, long life history. They invest substantially in their own embodied capital (e.g. size in general, or size of particular kinds of capital, such as brains and cognitive capacities) investments that pay off over time (i.e. are wasted if an individual dies before they pay dividends,

but reap substantial fitness benefits if used over a long lifespan). They also invest in somatic repair, which leads them to senesce relatively slowly. For such species, relatively risk-averse strategies with respect to threats of viability (e.g. predation, infection) should be selected [22]. For these species, then, the benefits of avoiding risk of infection by preferring non-infected mates should be relatively great.

Additional circumstances in which the benefits to infectious disease avoidance are relatively great include the following: (i) when disease is particularly prevalent and virulent; (ii) when mates interact repeatedly, as in instances of biparental care, as opposed to a one-shot mating; and (iii) when disease can lead to impaired reproduction, as in instances of STDs that cause permanent infertility.

(ii) When the direct benefits of care offered by mates are relatively great and compromised by disease
Species in which substantial levels of care for offspring have been favoured should particularly value mate health, because compromises in care imposed by infectious disease carry large fitness costs in the currencies of offspring viability or quality. Although these benefits select for preferences with the function of obtaining care rather than disease avoidance *per se*, both benefits can work in tandem to yield stronger preferences. In the light of coevolution between a slow life history and investments in offspring quality, these species should substantially overlap with those above, including species in which biparental care has evolved. In such cases, both sexes should often prefer healthy mates.

(iii) When health and genetic fitness positively covary and indirect benefits are relatively great
Preferences for mates that are currently disease-free and are expected to be disease-free in the future are expected to be strongest when these features positively covary and hence do not impose opposing selection pressures on mate preferences or force strong trade-offs between current health and health-proneness [1]. In turn, species in which condition, health-proneness and genetic fitness positively covary should be characterized by weak to moderate sexual selection, lying at the 'viability-indicator' end of Kokko *et al.*'s [8] sexual selection continuum. At the same time, indirect benefits of viability cues may be relatively weak when sexual selection is weak. Possibly, then, preferences for mates for the function of disease avoidance may be most pronounced in species in which sexual selection is of moderate strength: not too low for sexual selection to be important, and not too high for quality to be negatively associated with infection. Again, however, we emphasize that formal modelling may be needed to clarify expected associations between strength of sexual selection and preferences for health and health-proneness.

(iv) When encounter rates with members of the other sex are high
In general, choosiness increases as search and opportunity costs diminish (e.g. in circumstances of group-living or dense population), and the same should be

true of choosiness about mate health. Mutual mate choice can suppress choosiness among less-favoured members of the species and hence, here, one might often expect condition-dependent preferences in species with mutual mate choice or biparental care.

(v) *Bidirectional effects*
We have speculated about the circumstances that particularly favour the evolution of robust preferences for mate healthiness. As has been discussed in the literature [23], causality can run the other direction: once disease avoidance and preferences for healthy mates evolve, other features may follow. For instance, preferences for healthy mates may disfavour promiscuity and favour the evolution of pair-bonding [19,24]. More generally, then, one might expect the coevolution of bundles of features, of which preference for healthy mates is one feature. Once again, additional formal modelling or simulation of how features can be expected to coevolve would be useful.

(vi) *Summary*
Tentatively, we expect that species with a slow, long life history, substantial investments in embodied capital that pay off over time, extensive parental care, repeated interactions between mates and moderate strength of sexual selection are ones in which preferences for mate healthiness—both current health and health-proneness—for the function of disease avoidance should be relatively important. One such species is humans. As it happens, there is probably more research speaking to preferences for mate healthiness in humans than any other species. Hence, we dedicate much of our empirical review to literature on humans.

3. CUES AND SIGNALS OF HEALTH
To prefer a mate that is disease-free for the function of disease avoidance, individuals must have available to them features of others that covary with being free of or resistant to infectious disease. In general, there are two broad sorts of traits: cues and signals. Signals of being disease-free or health-prone are features that evolve for the function of communicating to others those states. Cues are observable features that happen to covary with a particular state, without any function to communicate ([25]; also see [25] concerning other pertinent topics, such as amplifiers and revealing displays).

(a) *Cues of infection status*
Some pathogens cause changes to the phenotype of the host, either as a direct result of the pathophysiology of the infection (e.g. open pus-oozing sores, dripping nasal mucus, sneezing) or as a function of adaptations of the host to combat the pathogen (e.g. fever). These changes may be detectable via visual cues (e.g. in the case of open sores, fever-induced pallor), auditory cues (e.g. the sound of coughing, sneezing and vomiting) and perhaps olfactory cues (e.g. the scent of vomit).

(b) *Cues of health, broadly defined*
In many species, individuals in good condition optimally allocate energy in ways different from individuals in poorer condition, such that a variety of phenotypic features discriminate between them. For instance, individuals in good condition may grow larger. Or, they may benefit from greater levels of intrasexual competition and hence invest more energy into features dedicated to competition, and they may be more willing to engage in these competitions. As well, individuals in good health may exhibit cues of abilities to defend against pathogens, independently of current infection status. In humans, for example, clear skin tone and complexion may partly reflect broadly defined health [26]. Cues of broadly defined health, unlike direct cues of infection status, need not specifically indicate current or future infection status. But because they may positively covary with current or future infection status, preferences for them may evolve for the function of disease avoidance (even if, in many instances, preferences for them also have other benefits associated with having a healthy mate, both direct and indirect).

(c) *Cues of ability to detect pathogens*
In vertebrates, major histocompatibility complex (MHC) alleles function to code for cell-surface markers used by the immune system to detect foreign pathogens. Relative to homozygosity, heterozygosity at these loci may lead an individual to be able to detect and thereby resist a greater diversity of pathogens. Certain MHC variations can be detected via chemical cues, e.g. in the urine of mice [27] or the scent of humans [28]. Preferences for MHC heterozygosity may thereby evolve for the function of detecting infection-proneness ([29,30]; see also §4*g*). Indeed, recent evidence indicates that the peacock's tail length partly reflects diversity at MHC loci [31].

(d) *Signals of condition or health-proneness*
Sexual selection, driven by mate preferences, may yield features that function to communicate (or signal) to others one's own condition or health-proneness. Specific selection processes that generate these preferences have received much attention from evolutionary biologists (for reviews, see [7,15]). Some features may evolve through these processes exclusively as signals, e.g. the peacock's tail. Preferences for others may first evolve because they are cues, but later become exaggerated through sexual selection, e.g. intrasexual competitive abilities.

Some have argued that preferences for sexually selected signals evolve largely for the function of avoiding infectious disease, such that the signals themselves communicate the signaller's current or future infection status, even if imperfectly [11–13]. In light of the multiple potential benefits of mating with individuals in good condition, however, it seems more likely that disease avoidance is one of several benefits that drive the evolution of these preferences.

4. COEVOLUTION OF HOST PREFERENCES AND PATHOGEN CUES
Mate preferences for health or condition that benefit the mate chooser in currencies of better care or genes for offspring have implications for selection on

both individuals possessing the preferences and on individuals that are their potential mates. Mate preferences that function to motivate pathogen avoidance also have implications for selection on the pathogens to be avoided. Pathogenic transmission rates are lowered when hosts are selected to prefer non-infected mates. Selection on pathogens, then, may favour those that do not cause cues of infection, i.e. those that cryptically infect hosts.

Such selection pressures are conceivably especially strong on STDs, for the simple reason that STD transmission relies exclusively or heavily on their hosts having sex, which, in turn, importantly relies on their hosts being selected as mates. Hence, one might expect sexually transmitted pathogens often to infect hosts cryptically [17–20]. Cryptic infections yield few or minor cues of infection, thereby limiting information on which mate choosers could act to avoid mating with infected individuals. As a byproduct, cryptic infections may also tend to be of relatively low virulence. Mildly virulent infections may tend to compromise the host's condition only in minor ways, such that hosts are unlikely to evolve condition-dependent costly signals strongly associated with current infection by the STDs. Hence, Knell [17] argued, contrary to Loehle [13], that sexually selected costly traits are unlikely to function to signal being free of infection by a sexually transmitted pathogen.

Even when mate choosers do not have the ability to detect and hence avoid STDs because of their cryptic, low-virulence status, STDs can nevertheless affect the evolution of mate preferences. As noted above, in some mating systems individuals that possess well-developed signals actually have a greater chance of currently being infected with a contagious, infectious disease. The circumstances receiving greatest attention in the literature are ones involving STDs, whereby attractive individuals (e.g. those with well-developed signals of condition) are more likely to be infected by virtue of their number of sexual partners. When these diseases are cryptic and hence undetectable by mates, they may nonetheless affect preferences, as they increase costs of and attenuate preferences for attractiveness [18,19]. Furthermore, the value of preferences for attractiveness varies by their frequency; as the preferences become rare, attractiveness becomes less strongly associated with STDs and preferences become more valuable. Models show that substantial variation in preference for mate attractiveness—with some individuals varying in their willingness to risk STD infection by mating with attractive individuals—can thereby be maintained by negative frequency-dependent selection [18,19].

5. PREFERENCES FOR HEALTH IN HUMANS

As noted above, we pay special attention to humans given (i) the abundance of empirical research concerning human mate preferences and disease avoidance and (ii) the expected emphasis on partner health in mates given human life history. We first briefly characterize human mating systems, and then review the human literature on preferences for health and suggest future research directions.

Humans have a relatively slow life history, with large, metabolically expensive brains, a long expected lifespan, substantial lifelong investment in embodied capital and a long juvenile period characterized by vulnerability and essential investment from adults [32]. Infectious diseases can significantly disrupt this strategy at multiple points. Among other things, pathogens can impede brain development and function, interrupt parental investment, and kill. Humans should thus invest considerable effort into avoiding infectious disease. Given the high infection risk associated with sexual interactions, humans theoretically gain substantial direct benefits by choosing mates possessing features indicating a lack of current infectiousness.

Although debate persists [33], substantial evidence has mounted in favour of the claim that human mating systems have ancestrally been and currently are typically characterized by pair-bonding and biparental investment in offspring [32,34]. Mates who are especially unhealthy may be more likely to acquire and transmit infectious disease to their partner over time, and their lack of health may compromise long-term investment in offspring in ways noted above. Hence, both sexes gain direct benefits, including disease avoidance, from choosing not only mates who are currently healthy but are also health-prone.

As previously discussed, health need not covary positively with genetic quality, as high-quality individuals may divert investment from immune function to intrasexual competition under certain conditions (e.g. conditions of strong reproductive skew). However, humans in many populations have only moderate reproductive skew [35] and intrasexual competition—or, at least, not so strong as to cause genetic quality to be associated with poorer viability [8]. Preferences for health and health-proneness may thus provide indirect benefits as well.

(a) *Assessing health in humans*

Infectious disease plays a critical role in the evolution of mate preferences based on health. Naturally, then, psychological adaptations for detecting and avoiding infectious disease should play an important role in assessing the health of potential mates and motivating adaptive behaviour. Humans have evolved to detect infectious disease threat via tactile, olfactory and visual cues that have reliably connoted pathogen presence over evolutionary time [36–43]. For instance, open, inflamed pus-oozing sores indicate infection, and people typically respond to these features in strangers by withdrawal, which is often accompanied by a visceral emotional response in the domain of 'disgust' [44,45]. These cues are used to assess infectious disease threats posed by conspecifics in general, and they presumably play an important role in mate choice. Individuals possessing cues associated with infection should be proximally avoided in general, but they should especially be avoided as mates, as pair bonds generally involve repeated interactions (and opportunities for pathogen transmission) and sexual interactions, which are especially infectious. Moreover, infection cues may indicate long-term

immune deficits which may depress potential for investment and, if heritable, may further compromise offspring fitness.

Although systems designed to detect pathogen threats in the general ecology are necessary, they are likely not sufficient for assessing health in mates. For example, current infectiousness, while important, does not fully encompass human health. Several cues used to detect immediate pathogen threats (e.g. odours associated with pathogenic bacteria) may not meaningfully inform long-term immune function and, and hence other features may be used to assess long-term pathogen susceptibility [46].

(b) *Physical attractiveness and health*
Mate 'attractiveness' evolves through selection on mate choosers [47], and selection should have favoured attraction towards those features that are valuable in mates. If health is valuable in mates, as is likely the case, then attractive features should partially indicate health [46,48,49]. Studies have repeatedly supported this prediction by demonstrating that faces rated as 'healthy' are also rated as more physically attractive [50–53]. We note that such findings could be methodological byproducts of valenced responses to faces (halo effects). That said, some empirical evidence does suggest that physical attractiveness conveys objective health-relevant information. For example, Gangestad *et al.* [54] found that individuals rated as more physically attractive have lower oxidative stress, which is associated with several serious health problems, and Henderson & Anglin [50] found that physical attractiveness covaries with longevity, which may relate to health. Nevertheless, the evidence for relationships between perceived physical attractiveness and health or actual immunocompetence is inconsistent [51,55].

Regardless of the existence of a relationship between health and physical attractiveness, physical attractiveness is an insufficiently precise attribute to reveal the cues used to assess health. It need not reflect a single, coherent set of features, as selection may have shaped individuals to find certain people attractive for functionally disparate reasons. Two individuals may be equally attractive, yet owing to different features (e.g. one owing to health cues, the other owing to cues completely unrelated to health).

Conversely, features valued in mates need not be reflected in what people refer to as physical attractiveness. Mate value is influenced by several traits, some of which may not be related to physical attractiveness (e.g. resource control, willingness to care for offspring). And, as discussed earlier, high-quality organisms may trade energetic investment in health for investment in intrasexual competitive ability, and physical attractiveness may reflect signals or cues of competitive ability rather than health.

(c) *Sexual dimorphism and health*
Theoretically, secondary sexual traits such as facial masculinity (e.g. pronounced brow ridge and well-developed chin in humans) may signal health via mechanisms proposed by Folstad & Karter [56]:

only individuals with especially robust immune systems may be able to withstand the energetic and potentially immune-suppressing effects of the sex hormones necessary for developing such traits. These associations receive some empirical support. Using facial landmarks that differentiate men and women, Thornhill & Gangestad [57] found that facial dimorphism covaries with self-reports of frequency of respiratory infection (though not gastrointestinal infection) over the past 3 years among college undergraduates. Men with greater facial masculinity reported fewer respiratory infections ($r = -0.19$), and women with greater facial masculinity reported more respiratory infections ($r = 0.18$).

At the present time, however, there is little reason to believe that the advantages of mating with individuals that invest in these reproductive traits are specific to immunocompetence [15]. Individuals in best condition, broadly conceived, may be best able to invest in reproductive traits, which secondary sexual traits may represent. As we have noted repeatedly, individuals currently in best condition may or may not be the most healthy in the future. Indeed, the sexually dimorphic facial traits typically measured reflect investment in a dimorphic phenotype during adolescence, and need not reflect adult condition [53]. Men's investment in masculine traits, in particular, has recently been argued to represent mating effort, including willingness and ability to engage in potentially costly intrasexual competition [58]. Current investment in these forms of mating effort (and perhaps past somatic investment in sexually dimorphic traits) could negatively affect health, including proneness to infection, in the future.

(d) *Skin colour and texture*
Skin tone and texture may convey important information about underlying metabolic health and infectious disease status, presumably because it relates to blood oxygenation and skin vascularization [26,53,59]. Facial attractiveness covaries with health ratings of isolated facial skin patches viewed apart from other facial features such as symmetry and dimorphism [53,60,61], and objectively measures skin characteristics such as colour (e.g. redness and yellowness), and haemoglobin and melanin homogeneity impact perceptions of health and attractiveness across multiple face ethnicities [26,62]. Additionally, skin colour may inform carotenoid concentration, which may reflect resistance to infectious disease and oxidative damage [63], though there is currently little direct support for the idea that carotenoid concentration in human skin reflects adaptation to advertise robustness in the way that concentrations of carotenoids in colourful bird feathers may do [64]. Indeed, at the current time, little direct evidence addresses whether skin tone or colour reflects current infection levels or infectability. More research is clearly needed.

Ratings of healthiness of men's and women's faces, which appear to reflect variations in skin tone and texture, do not strongly covary with measures of masculinity or femininity of the same faces [65], indicating that these dimensions largely reflect different qualities.

(e) Facultative shifts in preferences for health

Preferences for health in mates can be costly. Minimum standards for health may entail greater investment in search time and lead to rejection of mates otherwise of high value. Degree of health preferences should thus vary as a function of the benefits gleaned from choosing healthy mates and preference-related costs, which may vary across contexts. Several studies on humans reveal context-dependent facultative shifts in preferences for health or traits that plausibly advertise health.

Some research has suggested that perceptions of vulnerability to infectious disease covary with preferences for health in faces. Individuals who score higher on the perceived vulnerability to disease scale (PVD; [66]), which purportedly reflects behavioural avoidance of pathogen threats, demonstrate greater preferences for faces morphed to appear healthy versus unhealthy [67]. This conceivably reflects a greater investment in the direct benefits of not being infected, either during copulation or repeated interactions within a pair bond. Assuming heritability of health, this association could also reflect greater weighting of the indirect genetic benefits conferred by a mate's health among individuals who perceive disease threats as more dire. Finally, if PVD reflects a greater belief that infectious disease is a threat to viability, then increased preferences for healthy faces could reflect concerns that infectious disease could impair a mate's ability to invest in offspring in the future. Currently, little is known about the conditions that lead individuals to perceive themselves vulnerable to disease; hence, the benefits and costs that lead to associated face preferences remain unclear.

Women's sensitivity to pathogen disgust (as measured by the three domain disgust scale [42]) covaries with preferences for facial masculinity in morphed and unmanipulated male faces [68]. If sensitivity to pathogen disgust reflects investment in avoiding infectious disease threats, then this finding may reflect a greater prioritization of the direct benefits (e.g. avoiding infection) offered by men with masculine faces, who may be less likely to carry an infectious disease [57]. Alternatively, if sensitivity to pathogen disgust reflects an implicit perception of pathogen threat in the local ecology, the finding may reflect a prioritization of indirect benefits offered by men with facial masculinity.

Shifts in ecological conditions may also alter the costs and benefits of health preferences in potential mates. If health-relevant challenges appear (e.g. pathogen threats), then features relevant to health may increase in value. Indeed, Little *et al.* [69] report that, after exposure to visual pathogen primes, which presumably communicate increased threat of infectious disease, research participants demonstrate increased preferences for symmetry and sexual dimorphism in opposite sex—but not same sex—faces. The cross-sex nature of these shifts in preferences for symmetry and sexual dimorphism, both of which may indicate health or health-proneness suggests that infectious disease cues may increase preferences for health in mates in a manner different from general social partners. Once again, however, it is

unclear whether putative adaptations responsible for facultative shifts evolved via direct benefits (e.g. pathogen avoidance) or indirect genetic benefits.

Menstrual cycle shifts in mating psychology may speak to the issue of whether direct or indirect benefits drive preferences for traits potentially related to health. A rich literature describes adaptive shifts in women's mating psychology to increase attraction to particular male attributes when fecundability is high (for reviews, see [70–73]): e.g. increased preferences for intrasexually competitive behaviour [74,75], masculine faces, bodies and voices [75–78], and the scent of symmetric men [79–81]. Interestingly, these preference shifts across the cycle are specific to women's judgements of men's sexiness (or desirability as a short-term partner), not their attractiveness as long-term, investing mates. It has been argued that women's oestrous mate preferences weigh cues and signals of intrinsic genetic benefits more heavily than their preferences outside of the fertile phase; oestrous sexuality arguably evolved to possess functions different from women's non-conceptive sexuality [72]. This argument proposes, then, that women's mate preferences for a variety of masculine features function most markedly to acquire mates of high genetic quality rather than motivate disease avoidance.

And indeed, evidence about what women prefer during non-fertile phases (e.g. the luteal phase) bolsters this claim. Normally cycling women find healthy face morphs more attractive in the luteal phase than in the late-follicular (fertile) phase of the cycle, independently of other facial features (e.g. masculinity; [82,83]). More generally, women appear to engage in greater levels of disease-avoidance behaviour during the luteal phase [84–86]. The luteal phase is characterized by increased progesterone levels, which lead to a thickening of the uterine endometrium, which in turn allows for blastocyst implantation. It has been argued that women adaptively downregulate immune function during this phase to protect the blastocyst from attack, and engage in disease-avoidance behaviours to avoid contact with pathogens during this sensitive period [84]. Alternatively, the effects of progesterone during this phase may be byproducts of disease-avoidance adaptations for pregnancy, which is characterized by very high levels of the hormone [82,83]. Finally, diminished levels of disease-avoidance behaviour during the fertile phase relative to the luteal phase may reflect increased willingness to risk contact with pathogens as a trade-off to benefits garnered through mating with high-quality males.

In sum, documented changes in women's preferences across the menstrual cycle suggest at least partially distinct functions of preferences for sexual dimorphism and healthy appearance (e.g. healthy-appearing skin tone). The latter appears to function more strongly as a means of avoiding infectious disease.

Recently, Scott *et al.* [53] demonstrated that skin colour, rather than objectively measured facial masculinity, has a strong influence on women's attractiveness ratings of men's faces. In the light of results above, these results may suggest that women's attractiveness judgements (and perhaps women's mate preferences in general) place a greater emphasis on direct benefits

compared with indirect benefits of health in mates—though they may value the latter variably across their menstrual cycles as well as, perhaps, their own condition [87].

(f) *Cross-cultural variation in mate preferences*

Laboratory-based studies examining individual differences and the effects of experimental manipulations suggest that health preferences in mates vary across individuals depending on pathogen threats, either real or perceived. Cross-cultural studies lend further support to this hypothesis. Gangestad & Buss [88] found that, across nations, parasite prevalence covaries with the degree to which physical attractiveness is prioritized in mate choice. This effect persists even when controlling for other variables, such as nations' gender equality [89]. In addition, nations' parasite prevalence positively relates to mate preferences for health, status striving (i.e. intrasexual competitiveness), which may relate to health via covariation between quality and immunity, and intelligence, which could reflect resistance to pathogens during brain development [90]. DeBruine et al. [91] observed a relationship between nations' health (as assessed by mortality rate and life years lost to infectious disease) and women's preferences for male facial masculinity in men, though the robustness and meaning of this association has been questioned [92,93]. In any event, it is not clear that these preference shifts reflect adaptation for disease avoidance. Indeed, as noted above, enhanced preferences for male masculinity may reflect willingness to risk contact with pathogens as a trade-off for mating with a high-quality mate, a trade-off that could evolve in response to high extrinsic mortality. At the same time, Fincher and co-workers have argued that humans facultatively respond to cues of prevalent parasites by engaging in a variety of disease-avoidance strategies, most notably by avoiding contact with people not adapted to extant parasites [94–98]; see also [99]. (See also Denic et al. [100] on how purported increases in resistance to malaria in offspring of consanguineous couples may lead to increases in cousin marriages in areas with increased malaria.) More research is needed to fully make sense of cross-cultural patterns of health-relevant mate preferences.

(g) *Major histocompatibility complex preferences*

As noted earlier, heterozygosity of MHC alleles may yield abilities to resist a greater range of pathogens relative to homozygosity. Indeed, heterozygous MHC is associated with greater resistance to multiple infectious diseases in human populations, including HIV [101], human T lymphotropic virus [102] and hepatitis B [103]. Individuals could prefer mates with greater levels of MHC heterozygosity for direct benefits, including avoidance of infectious disease, either current or during future interactions and ability to care for offspring. Thornhill et al. [81] found that women exhibited strong preferences for the scent of MHC heterozygous men (cf. [104]), but they found no comparable preferences in men. Similarly, Roberts

et al. [61] and Lie et al. [105,106] reported that women prefer faces of men who are heterozygous at MHC loci, an effect that Roberts et al. [61] suggest may be mediated by healthier skin tone.

MHC heterozygosity, though a genetic trait, cannot be passed directly from parent to offspring; each parent, of course, passes on just one of their alleles at each locus. Hence, MHC heterozygosity in a mate does not represent an intrinsic genetic benefit that can be passed on to an individual offspring. However, repeated reproduction with a heterozygous mate, relative to a homozygous mate, would yield a more diverse family of offspring. In turn, a diverse set of siblings could be less likely to acquire diseases from each other, as they would be resistant to different diseases. Interestingly, then, Thornhill et al. [81] also found that women tended to prefer the scent of MHC heterozygous men more so during the non-fertile phases than during the fertile phase of the cycle (though the effect fell just short of a conventional level of statistical significance). Further research is necessary to establish the reliability and meaning of this finding.

Though male preferences for MHC heterozygosity in women have not been documented, Thornhill et al. [81] reported that men prefer the scent of women possessing common (as opposed to rare) MHC alleles. Subsequently, Coetzee et al. [107] found that women in a South African population with common MHC alleles report fewer cold and flu bouts in a year, and rate themselves as healthier. Both direct benefits (e.g. disease avoidance) and indirect benefits could drive male scent preferences.

Whereas mate preferences for MHC heterozygocity may confer direct benefits, preferences for MHC dissimilarity may provide indirect, genetic benefits. Because individuals with dissimilar alleles are more likely to produce MHC heterozygous offspring, preferences for MHC dissimilarity may confer immunocompetence to offspring [108]. Studies of naturally reproducing human populations (populations without hormonal contraception) have provided mixed evidence for disassortative mating based on MHC [109–111]. Preferences for the scent of opposite sex individuals with dissimilar MHC genotypes have been detected in three of four studies of normally ovulating women ([112–114]; cf. [81]) and two of three studies of men ([81,113]; cf. [114]). (In another study, women preferred the scent of MHC-similar men, but its preference measure may not tap sexual attraction [115].) In a study of pair-bonded American couples in which the female was normally cycling, women paired with men with whom they shared relatively many MHC alleles reported being less sexually responsive to their mates, and they reported experiencing greater attraction to men other than their mates, particularly when in the fertile phase of their cycles [116].

(h) *Sexual disgust*

As argued by several authors contributing to this special issue, disgust is an emotional reaction that likely evolved as an adaptation for disease avoidance. People react to visual, olfactory and tactile cues of infection sources with an aversive response, often

captured by the emotion of disgust. But as multiple researchers have noted, disgust is also elicited by other features [42,99,117–119]. Tybur *et al.* [42] found evidence for distinct individual differences in sensitivity to disgust in three domains: pathogen avoidance, sex and morality. Disgust sensitivity in any one domain covaries only modestly with sensitivity in the other domains (mean *r* approx. 0.3).

Sexual disgust items in Tybur *et al.*'s three domain disgust scale concern aversion to a variety of sexual content outside of intercourse in a close committed relationship: hearing strangers have sex; seeing a stranger naked; having someone brush one's thigh in an elevator; bringing a stranger home to have sex knowing they will never be seen again. Sexual disgust may largely function to avoid sex that compromises one's own fitness. As women arguably pay larger fitness costs for conceiving an offspring with someone other than a close, committed relationship partner, someone whose phenotype they have had sufficient opportunity to examine for quality and compatibility and someone who carries a communicable disease, it makes sense that they would experience substantially greater levels of sexual disgust than men. And, indeed, women score only mildly higher on the pathogen and moral subscales of the three domain disgust scale (Cohen's *d*'s ranging from 0.15 to 0.32; [42,120]), but much higher on the sexual subscale (Cohen's *d* above 1.00).

Though by no means specific to pathogen avoidance, avoidance of fitness-compromising sex may include avoiding sex with individuals who carry pathogens. All else being equal, then, individuals with greater sensitivity to sexual disgust are particularly avoidant of infected mates. Interestingly, in this light, Tybur *et al.* [42] found that PVD predicts sensitivity to sexual disgust just as strongly as it predicts sensitivity to pathogen disgust.

As we previously discussed, STDs may evolve to be cryptic, such that cues of infection are largely lacking. Even in such cases, however, STDs may exert selection on mate preferences. Specifically, selection may attenuate preferences for certain otherwise desirable mates (e.g. more masculine men) if they are more likely to carry STDs because they are generally preferred, and hence have a greater number of sexual interactions and partners. Modelling shows that frequency-dependent selection may maintain variation in preferences for these individuals. Sensitivity to sexual disgust is strongly related with willingness to engage in sex outside of committed relationships (e.g. sociosexual orientation; [121]). Women who find uncommitted sex particularly averse (those of restricted sociosexual orientation) report that they value male attractiveness and status less than women open to uncommitted sex [122]. Though this finding has been interpreted as reflective of individual difference in how genetic benefits are traded off against direct benefits of paternal investment [123,124], it is also possible that it reflects, at least partly, a trade-off between male quality (e.g. genetic benefits) and risk of exposure to STDs. This possibility has not been systematically assessed (but see also [91]).

6. SUMMARY

In sum:

— Research clearly indicates that people prefer mates partly on the basis of cues or signals of health or health-proneness. In addition to overt signs of infectious disease, people prefer mates partly on the basis of sexually dimorphic features, symmetry, skin tone and colour—characteristics that research has linked with measures of health. Research suggests that people also prefer in mates features associated with MHC heterozygosity or common alleles (though perhaps differently across the sexes), which are linked with resistance to infectious disease. Additional research is needed to establish more firmly associations of preferred features with health, health-proneness and specific contributions to health (e.g. immune recognition, immune responsiveness, oxidative stress).

— Preferences for these health-related features, however, could provide multiple benefits, both direct material benefits and indirect genetic benefits. The extent to which the preferences function to avoid disease (that is evolved through selected advantages associated with disease avoidance *per se*) remains unclear. The best inference possible now is that preferences for sexually dimorphic features (perhaps particularly male ones) evolved at least partly to obtain indirect genetic benefits for offspring (indeed, they appear to be highly conditional on circumstances that magnify the importance of those benefits). Preferences for skin tone and MHC variants are more likely to have been selected for disease avoidance *per se*, though alternative benefits are also likely candidates. Preferences for the absence of overt signs of disease likely do function for disease avoidance, but, to date, have received very little attention from researchers.

— Researchers have fruitfully studied the context-dependent nature of mate preferences for health-related features (e.g. as they vary across women's menstrual cycles and cross-nationally). The context-dependent nature of preferences offers one window into the design and hence function of the preferences. Despite a growing literature addressing these matters, many questions about context dependence remain.

— Related to context dependency, a variety of individual differences are associated with specific preferences and the propensity to experience disgust in the context of sexual relations more generally. Theory offers reasonable suggestions about what causes individual differences to arise (e.g. disease-proneness, frequency-dependent selection); little research to date has addressed these suggestions.

— Similarly, little research to date has examined in humans the ways that STDs have shaped particular mating preferences and propensities, despite obvious implications of STDs for these matters. Even if STDs are largely cryptic owing to selection on them, they may have exerted important selective pressures.

(a) *Concluding remarks*

As summarized by other articles in this special issue, infectious disease has constituted a strong selection

pressure and engendered the evolution of multiple disease-avoidance adaptations. Given the high potential for pathogen transmission between mates, disease avoidance may have an especially strong influence on mate preferences. Additionally, unique aspects of mating relationships (e.g. influence of partner heritable immunity on offspring fitness) may lead to greater, unique emphasis on health in mate preferences. In this paper, we have detailed the various types of benefits to selecting mates based on health, as well as the costs that may constrain preferences for health. We hope that this summary offers a productive framework with which to build upon past research on human and non-human mate preferences, and with which to disentangle the degree to which mate preferences reflect various aspects of disease avoidance versus other valuable traits.

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