Many species rely on chemical signals to attract and select mates (Box 1). The scent glands, scent-marking behavior and pheromones that transmit chemical signals are often sexually dimorphic, even in species in which the sexes are visually similar or show no other conspicuous dimorphisms (Fig. 1). Darwin suggested that the exaggerated displays of males, including ‘glands for emitting odours’, evolved through sexual selection (cited in Ref. 2). Females direct their attention to male odors, which convey a surprising amount of information, such as a male’s dominance status. The chemical signals of a male might also advertise health or genetic quality to prospective mates (Box 2). Hamilton and Zuk suggested that females prefer to mate with males with showy sexual displays because they are the healthiest and the most resistant to parasites. By avoiding infected males, choosy females can reduce their risk of contracting contagious diseases, obtain more parental investment and increase the resistance of their progeny to parasites.

Numerous studies have found that a male’s secondary sexual displays honestly reveal his parasite load. Research on parasite-mediated sexual selection, however, has focused almost exclusively on visual and acoustic signals, ignoring chemical communication. Chemical signals could provide particularly effective indicators of an individual’s health and infection status because they are direct and often more reliable than morphological traits. Physicians and veterinarians have long used the taste and smell of a patient’s body odor, breath, urine and flatulence to diagnose disease (Box 3 and Table 1). Furthermore, chemical signals provide information about an individual’s genetic compatibility at loci that control immune recognition of parasites.

Parasitic infection abolishes the attractiveness of male scent

Male house mice (Mus musculus) scent-mark with urine, and females are attracted to these marks. Recently, Kavaliers and Colwell found that female mice can discriminate the odors of parasitized from unparasitized males. Additional odor-preference experiments have shown that females not only discriminate, but are also more attracted to the odor of uninfected males than those males experimentally infected with parasitic coccidian protozoans (Eimeria vermiformis) or nematode worms (Heligmosomoides polygyrus). To test whether females were detecting infection from a male’s urine odor (e.g. via metabolic by-products and scent glands) or simply from components of the parasites shed in the male’s feces, we recently conducted an experiment using the urine from male mice collected before, during and after being experimentally infected with influenza, a respiratory virus. We found that females were more attracted to a male’s urine before and after infection than while he was combating the infection. Moreover, females were more likely to settle in nest boxes containing the scent of a male when he was uninfected than when he was infected.

Research into visual and acoustic signals has demonstrated that exaggerated sexual displays often provide an honest indicator of a male’s resistance to parasites. Recent studies with rodents and humans now suggest that chemosensory signals also reveal a male’s disease resistance and his genetic compatibility. Our understanding of sexual selection has been greatly enriched by considering the mechanisms underlying visual and acoustic displays, and recent advances in chemical communication will help to determine what kind of information is revealed by an individual’s scent.

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**Box 1. Chemosensory sexual displays**

Chemical communication between the sexes occurs in many species: bacteria, protists, fungi, plants and animals all use chemical signals to attract and select mates. There is an enormous diversity of mechanisms mediating chemical communication, and these are often sexually dimorphic for both the sender and the receiver.

Single-celled organisms and the gametes of multicelled organisms use chemical signals to locate and recognize their mates. When male Danaus butterflies court females, they position themselves in front of the female and extrude a pair of elaborate structures called ‘hairpencils’ to display their chemical signals. When male blue crabs (Callinectes sapidus) perform their elaborate courtship display, they use their swimming legs to waft odors towards attentive females. Female lampreys (Petromyzon marinus) are attracted to testosterone and other odors in a male’s urine. The elaborate courtship behavior of salamanders, such as Notophthalmus viridescens, is centered around males rubbing or fanning odors secreted by various ‘hedonic’ glands onto a female’s nostrils or body. Male lizards, such as Iguana iguana, release sexual odors through large, femoral glands, whose secretions reveal much information, including their androgen levels and dominance status. Male mammals display their scent for females using complex mixtures of odors secreted by a variety of androgen-dependent scent glands. A male’s odor has remarkable effects on a female’s reproductive physiology and behavior, such as accelerating puberty, activating ovulation, accelerating and synchronizing estrus, and inducing pregnancy block.

Despite these and numerous other examples, we still understand very little about the functions of chemical communication. Sensory biologists often assume these signals function only for species recognition or to coordinate mating between the sexes; they have largely been unaware of the advances in understanding the evolution of signal–receiver systems. At the same time, students of parasite-mediated sexual selection have focused on a small group of animals (mainly birds) and have ignored the chemical senses.
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Box 2. Honest signaling and the strategic-choice handicap model

Zahavi suggested that females use the elaborate sexual displays of males to assess their quality because such displays are costly and therefore cannot be easily faked. Only males of high quality can afford to support such a handicap to survival (e.g. a peacock’s elaborate train).

Initially, this counter-intuitive idea had little support among researchers because it seemed that choosy females would pass the male’s handicap, as well as his good genes, to her progeny, so both females and males would be better off without exaggerated ornaments. Grafen showed that sexual handicaps can evolve to display a male’s quality honestly if males have a mechanism that allows them to adjust their investment in sexual displays strategically, according to their condition. (Previous attempts to model the handicap theory failed because they only allowed the presence or absence of a display; they did not allow males to choose from a continuous range of strategies.) Grafen’s ‘strategic-choice handicap’ model is consistent with the hypothesis that males adaptively allocate energy and resources between sexual displays and immunological defences (the adaptive allocation hypothesis). Although a male’s odoriferous secretions might be a handicap to survival, they do not necessarily have to be costly to reflect health honestly. Metabolic wastes must be excreted, and it might be physiologically impossible (or too costly) for a sick animal to fake a healthy odor.

How does a male’s odor reveal his infection status?

There are many ways that an individual’s odor might signal infection. First, infection might change the composition of commensal microbes that play an important role in shaping an individual’s odor.

Second, infection might also trigger immunological responses that alter an individual’s odor. For example, the highly polymorphic genes of the major histocompatibility complex (MHC) control immunological self/nonself-recognition and also influence individual odor and mating preferences in mice. Because the expression of MHC genes is increased during infection, the MHC might play a role in honestly signaling the activation of immune defences. Although it is still unclear how MHC genes alter odor, a recent study found that they influence the concentrations of various volatile acids that serve as sexual odorants (‘copulins’) in mammals. The composition of these volatile acids appears to be altered during the course of infection, although it is unknown how this occurs.

Third, activation of the immune system probably alters the excretion of other metabolic by-products from the endocrine system. For example, infected individuals have high concentrations of plasma corticosterone and low concentrations of androgens, hormones suspected to control the production of ‘alarm odors’ and ‘sex pheromones’, respectively.

If females are detecting chemical cues from the immune system or stress responses, then why does the odor of infected males simply lose its attractiveness, rather than being aversive? One explanation is that a normally attractive odorant is absent in the urine of infected males. Androgen metabolites and secretions from androgen-dependent glands might provide such an odorant because increased androgen levels increase the attractiveness of a male rodent’s urine odor to females, and androgen levels generally decline during infection. Infected males might lower their androgen levels to ameliorate the immunosuppressive effects of these steroid hormones or to act as a signal to reallocate energy and resources into immune responses – better to be a dull-smelling male than a dead male! Decreased androgen levels can also result from manipulation by parasites that benefit by diverting their host’s reproductive efforts into their own reproduction. If a male’s androgen levels generally decrease during infection for any reason, then his parasite load will be revealed honestly by his androgen-deprived odor.

Androgens and the immunocompetence handicap hypotheses

Androgens, such as testosterone, control the development of many secondary sexual characters, but why would sex hormones suppress the immune system? Folstad and Karter proposed that androgen-dependent signals provide honest indicators of a male’s health because of the immunosuppressive effects of androgens. However, they assumed that the adverse effects of androgens were an unwelcome byproduct or unmodifiable constraint. Androgens are simply chemical messengers, with one of their functions being to trigger the development of secondary sexual traits. If androgens are actually immunosuppressive per se, then it is difficult to understand why males cannot evolve a nonimmunosuppressive sex hormone, convert androgens into a nonimmunosuppressive form, or abolish the sensitivity of immune effectors to androgens. None of these possibilities would seem to be insurmountable evolutionary steps.

Recently, it has been suggested that testosterone is immunosuppressive because it prevents autoimmune attacks on developing sperm in the testes that express novel antigens, implying that the immunosuppressive effects of androgens on systemic immunity is a tradeoff to protect sperm from the immune system. However, this hypothesis assumes that testosterone ‘overflow’ into the rest of the

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body is unpreventable or that testosterone cannot be converted to a nonimmunosuppressive form when it enters the blood–testes barrier and peripheral immunological tolerance mechanisms, but it is unclear that testosterone is uncontrollable or unconvertible. This hypothesis seems to substitute one unlikely, unexplained constraint for another.

It is likely that androgens allocate energy and resources between reproductive functions and immunological defenses (the adaptive reallocation hypothesis)\(^{26}\). There is an inescapable tradeoff between survival and reproduction. To allocate energy into immunological defenses, infected males may be forced to reduce the costs of sexual displays by lowering androgen levels. The costs of both sexual displays and immunological defenses seem metabolically expensive; thus, it is surprising that chemical signals have not received more attention as potential disease indicators by students of sexual selection.

### Table 1. Body odor is a diagnostic indicator for many diseases

<table>
<thead>
<tr>
<th>Disease</th>
<th>Description of odor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Infections</td>
<td></td>
</tr>
<tr>
<td>Scourge</td>
<td>Sweat has putrid odor</td>
</tr>
<tr>
<td>Diabetic ketosis</td>
<td>Breath and sweat has the fruity aroma of decomposing apples</td>
</tr>
<tr>
<td>Gout</td>
<td>Sweat has a characteristic odor</td>
</tr>
<tr>
<td>Schizophrenia</td>
<td>Fungent body odor from increased trans-3-methyl-2-hexanoic acid in the sweat</td>
</tr>
<tr>
<td>Phenylketonuria</td>
<td>Musty odor, resembling stale, sweaty locker-room towels</td>
</tr>
<tr>
<td>Defective metabolism of amino acids (valine, leucine and isoleucine)</td>
<td>Maple syrup or caramelized sugar in sweat, ear wax, and urine</td>
</tr>
<tr>
<td>Inability to metabolize methionine</td>
<td>Breath, sweat and urine smells like boiled cabbage</td>
</tr>
<tr>
<td>Hyperaminoaciduria</td>
<td>Dried malt or hops (cast house syndrome)</td>
</tr>
<tr>
<td>Inability to metabolize butyric and hexanoic acids</td>
<td>The odor of sweaty feet syndrome</td>
</tr>
</tbody>
</table>

Physicians have long used odor to diagnose various diseases (Table 1), as illustrated in this woodcut. Nearly two centuries ago, one of the originators of Hindu medicine, Susruta Smintha, claimed that "by the sense of smell we can recognize the peculiar perspiration of many diseases, which has an important bearing on their identification." In one thousand years ago, the Arab physician Avicenna observed that an individual’s urine odor changed during sickness. Physicians once tasted a patient’s urine to diagnose diseases. For example, diabetes mellitus (which means ‘passing through sweet’) was once diagnosed by a patient’s sweet urine and for centuries the disease was called ‘passing’ or ‘visiting’. Vitamins often use faeces and other odor cues to diagnose diseases, such as toxins, ketones. Technological devices are currently being developed to diagnose disease from breath and other odor samples. Fisher long ago pointed out that bad breath may be sexually unattractive because breath is associated with various diseases.\(^{17}\) Hamilton and Zuk suggested that when females are inspecting potential mates they should, like physicians, ‘unclothe the subject, weigh, listen, observe vital capacity, and take blood, urine and fecal samples’. Thus, it is surprising that chemical signals have not received more attention as potential disease indicators by students of sexual selection.

**Box 3. Odor and diagnosis of diseases**

Physicians have long used odor to diagnose various diseases (Table 1), as illustrated in this woodcut. Nearly two centuries ago, one of the originators of Hindu medicine, Susruta Smintha, claimed that "by the sense of smell we can recognize the peculiar perspiration of many diseases, which has an important bearing on their identification". In one thousand years ago, the Arab physician Avicenna observed that an individual’s urine odor changed during sickness. Physicians once tasted a patient’s urine to diagnose diseases. For example, diabetes mellitus (which means ‘passing through sweet’) was once diagnosed by a patient’s sweet urine and for centuries the disease was called ‘passing’ or ‘visiting’. Vitamins often use faeces and other odor cues to diagnose diseases, such as toxins, ketones. Technological devices are currently being developed to diagnose disease from breath and other odor samples. Fisher long ago pointed out that bad breath may be sexually unattractive because breath is associated with various diseases. Hamilton and Zuk suggested that when females are inspecting potential mates they should, like physicians, ‘unclothe the subject, weigh, listen, observe vital capacity, and take blood, urine and fecal samples’. Thus, it is surprising that chemical signals have not received more attention as potential disease indicators by students of sexual selection.

**In addition to determining how infection alters a male’s odor, we must also determine how females detect, process and respond to olfactory information, because communication involves a signaler and a receiver (‘receiver psychology’)\(^{24}\). Understanding the design features of olfactory mechanisms will help to determine their function. Olfactory mechanisms, like chemical signals, are often sexually dimorphic\(^{25}\). Why is this? Sexual selection theory predicts that male chemosensory systems should be designed to locate females, whereas females, when they are the choosier sex, should be designed to discriminate the quality of males. Our understanding of chemosensory systems has lagged behind the visual and acoustic senses. However, recent advances using molecular tools are helping to determine how olfactory discrimination occurs. Progress on olfaction promises to have important implications for sexual selection, such as helping to determine how females discriminate the odor of infected and uninfected males.
Box 4. Measuring optimal immunocompetence

Immunocompetence refers to the ability of an individual’s immune system to resist and control infections. Various methods are useful for evaluating immunocompetence, including antibody response to an antigenic challenge, size of immune organs, lymphocyte counts and gamma globulin levels. There are several reasons why these assays might not accurately reflect an individual’s immunocompetence.

First, only a single component of the immune system can be measured because immunocompetence is a complex, dynamic trait. Infected hosts might sacrifice one or more immunological effectors for beneficial physiological responses for humoral ones. Also, assays that measure responses to foreign antigens indicate an ability to recognize foreign antigens, but they do not indicate other aspects of immune competence, such as the ability to detect cellular destruction (danger signals) during an infection. Using a single assay to measure immunocompetence is analogous to using small size in IQ to measure intelligence.

Second, it is often assumed that bigger is better when measuring immunological characteristics. But a bigger spleen or more lymphocytes can reflect infection rather than immunocompetence.

Third, immunocompetence assays also assume that maximal immunological responsiveness is better, but this is not necessarily the case. When mice are infected with the lymphotropic murine leukemia virus, the most immunosensitive mice die, whereas the lower responder survivors recover. The immune system is a double-edged sword. Immunological responses provide protection against parasites but they also cause immunopathology. T cells are cytotoxic, inflammatory cells release destructive chemicals, MHC complexes attack cell membranes, bacteria and mast cells release histamines, and misdirected antibiotics and T cells create autoimmunity. Launching an immune response to fight infection is like using chemotherapy to treat cancer; it can save your life but it also has some harmful side effects. The most immunocompetent individuals will optimize the benefits of immunological responsiveness and the costs of immunopathology. If a male’s sexual display reflects his optimal immunocompetence, rather than his maximal immunological responsiveness, then better methods will be needed to evaluate immune competence.

Finally, immunocompetence and resistance are often measured by parasite load, but this measurement does not necessarily reflect how well individuals cope with a parasitic infection.

Understanding how females respond physiologically to the odor of infected males could help explain why they lose their attraction for such odors. Kavaliers and Colwell’s studies on parasite-mediated odors in mice were prompted by a curious discovery: they made while investigating how chemical signals trigger neuroendocrinological responses in mice.

They found that when females are exposed to the odor of parasitized males they activate analgesic mechanisms that increase pain tolerance (via elevations in opioid (β-endorphins and enkephalins) and nonopioid (serotonergic) levels). Why do female mice increase their levels of endogenous opioids when they are exposed to the odor of infected males? There are several possible explanations.

First, Kavaliers and Colwell suggested that because opioid levels also increase during stressful situations, such as exposure to mice to the odor of restrained mice, odor-mediated analgesia is a part of a general stress response (proximate hypothesis) that functions to avoid disease transmission and mating with infected individuals (ultimate hypothesis). Their hypotheses are consistent with the observation that maximum analgesia occurs when females are exposed to odors collected from parasitized mice during the infective stages; but it is inconsistent with the observations that females do not treat the odor of infected males as aversive.

Second, odor-mediated analgesia might reflect a preparatory, defensive response against possible infections. Opiates are used to treat diarrhea (the intestine is rich with opioid receptors) – an aversive opioid-like effect might therefore be a useful defense against gut parasites (e.g. coccidia) that trigger debilitating diarrhea as a way to spread their infective stages. Analgesia might also reflect immunological preparation, because opioids can enhance immune responsiveness. The preparatory-defense hypothesis is not as far fetched as it might seem, because plants use chemical cues from infected conspecifics to activate preparatory defenses against infectious agents.

Third, increasing endogenous opioids might inhibit sexual receptivity (proximate hypothesis) to avoid mating with infected males (ultimate hypothesis). The use of opiate drugs in humans is well known to reduce sexual libido, and experiments indicate that increasing opioid levels can inhibit sexual receptivity (lethargy and estrus) in females. If odor-induced analgesia is part of a stress response or inhibits sexual receptivity, then either mechanism would support the sexual inhibition hypothesis. Sexually inhibited males might be more protective parents, and that might be the reason why males prefer to mate with females expressing dissimilar MHC genes. Studies of house mice under laboratory and natural conditions have shown that house mice prefer to mate with individuals expressing dissimilar MHC genes, and these preferences can be experimentally reversed through cross-fostering. How do mice recognize the MHC identity of potential mates? Numerous studies by Kunio Yamazaki et al. have shown that laboratory mice can be trained to detect odors of mice that differed genetically only at single MHC loci (reviewed in Ref. 7). We have recently found that wild-derived mice can discriminate the odors of MHC-dissimilar individuals. These studies indicate that rodents can recognize MHC identity of potential mates through specific odor cues.

Why do mice prefer to mate with MHC-dissimilar individuals? There are several ways that MHC-disassociative mating preferences might enable mice to increase the resistance of their offspring to pathogens and parasites.

• They will increase the MHC-heterozygosity of an individual’s progeny. MHC heterozygotes recognize a wider array of foreign antigens than homozygotes and therefore could be resistant to infections of multiple parasites.

• They might provide a moving target to rapidly evolving pathogens. Because pathogens evolve ways to evade MHC-dependent immunity, MHC-disassociative mating preferences might enable hosts to alter the immune systems of their progeny, shifting the targets of pathogen evolution.

• They might reduce inbreeding by increasing overall genetic heterozygosity, which is likely to increase disease resistance.
These mechanisms are not mutually exclusive. MHC-dependent mating preferences might enable individuals to obtain all of these benefits, although none of these potential functions has been adequately tested. Determining the ben-


Pheromones and mate choice in humans

Although humans are not known for their olfactory prow-


ommens. Unlike the main olfactory system, information from


pressing dissimilar MHC genes41. Our aim is not to exaggerate


senses, both taste and scent, during courtship and sex (in


perfume, of displays. Although an individual's odor does not need


function work on chemical signals and sexual selection should


Future directions

Chemical signals are used during mate choice in a wide
diversity of species and have been shown to honestly reflect
an individual's health7–10 (Box 3). However, it is unknown if
females use a male's chemical signals to avoid disease trans-
mision or to increase the resistance of their progeny. Fu-
ture work on chemical signals and sexual selection should
consider several important points.

First, females might attend to chemical cues that reveal
a male's previous, as well as his current, infection status.
Females might avoid infected males to avoid contracting
disease and infection sexually unattractive, and people liv-
ing in geographical regions with the highest risk of parasitic
infection value a male's physical attractiveness more than in
other areas36. Women prefer the scent of men with symmetri-
cal features, and body symmetry is often correlated with re-
sistance to parasites38. A recent study found that both men
and women prefer the odor of MHC-dissimilar individuals49,
and another found that couples tend to marry individuals ex-
pressing dissimilar MHC genes42. Our aim is not to exaggerate
the importance of pheromones in human sexual behavior but
simply to point out that chemical signals potentially trans-
mit more information than has previously been considered.

Fourth, females might use a male's chemical signals to
increase the resistance of their progeny via good parental
investment, rather than good genes. For example, females of
certain lepidoptera use a male's pheromones to assess
his stores of toxic alkaloids. During copulation, males trans-
fer the toxins to the female as a nuptial gift that females
incorporate into their eggs, which protects the eggs from
predators and parasitoids51.

Finally, more work is needed to determine how chemical
signals influence our own sexual behavior. Chemical signals
clearly affect human reproductive behavior and physiology,
although we are not consciously aware of their effects. For
example, women synchronize their menstrual cycles through
odor cues49, although they are not aware of the mechanism.
It is unclear why we are oblivious to our own chemosensory
communication, but perhaps our lack of awareness explains
why chemical signals have been neglected by students of
parasite-mediated sexual selection.

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