The evolution of female sex pheromones

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Abstract The role of female sex pheromones in natural selection, particularly as a means for species recognition to avoid the generation of hybrid offspring with low fitness, has been widely explored and is generally accepted by scholars. However, the significance of sex pheromones in shaping mate choice (sexual selection) and in competition over breeding resources (social selection) has been largely ignored. The effect of sexual selection on sex pheromones as a sexually dimorphic signaling trait has been discounted because the amount of pheromone released by females is typically minute, while the role of sex pheromones in competition over breeding resources (other than mates) has not yet been considered. As a result of natural selection, variation in sex pheromones among females is expected to be low, and males are not expected to choose their mates among pheromone-releasing conspecific females. Sexual selection, on the other hand, should drive the increase in pheromone variance among females, and males are expected to choose females based on this variation. Moreover, social selection resulting from more general social interactions, for example competition among females for breeding sites and food, should also promote variance among female sex pheromones. Here, we review the current evidence for each of the three selection processes acting on sex pheromones of female moths as an advertising trait. We suggest that the three selection types are not mutually exclusive but rather act together to promote different fitness components in diverse ecological situations [Current Zoology 59 (4): 569–578, 2013].

Keywords Sex pheromone, Natural selection, Sexual selection, Social selection, Competition, Mate choice

Pheromones are chemical signals produced by an organism that can elicit, even in small quantities, a behavioral or physiological response in another individual of the same species (Wyatt, 2003). Pheromones may be used for a variety of purposes. For example, pheromones may be used to alert conspecifics of danger, as information for orientation and foraging (Holldobler et al., 2001), to aggregate in attempt of resource exploitation (Borden, 1989) and as a social or recognition cue for kin or familiar individuals (Penn and Potts, 1999; Brennan and Kendrick, 2006). Pheromones are also used to attract or repel mates (for review, see Johansson and Jones, 2007), to mark territories (for review, see Mason and Parker, 2010), and to advertise the status or condition of the signaler (Olsson et al., 2003; Martin and Lopez, 2006; Harari et al., 2011). In general, pheromones are communication tools used by many taxa to convey information among individuals of the same species (Karlson and Luscher, 1959; Wyatt, 2003). Insects, in particular, have mastered the olfaction channel as a means for communication using volatile, task-specific substances. The properties of the pheromone allow for diverse information to be bounded to the receiver detecting and processing capabilities.

Researchers generally agree that sex pheromones, when are used to attract mates, provide information about the species and the gender of the signaler (Svensson, 1996; Johansson and Jones, 2007). However, the following questions about the nature of pheromones are still somewhat ambiguous. Are sex pheromones shaped by natural selection to prevent interspecific mating and the resulting production of hybrid offspring (Paterson, 1985; Löfstedt et al., 1991; Baker, 2002; Mas and Jallon, 2005)? Did pheromones evolve via sexual selection aimed at facilitating the competition for mates (Martin and Lopez, 2006; Harari et al., 2011)? Have sex pheromones evolved through social selection in the intraspecific competition over resources other than mates, such as direct competition for food and nest sites (Goekce et al., 2007; Harari et al., 2011; Tobias et al., 2012)? Is it possible that sex pheromones are affected by all three kinds of selection (natural, sexual, and social), depending on the species and the environment?

The debate on the distinctions between the different selection mechanisms began with publication of The Descent of Man, and Selection in Relation to Sex by Darwin (1871) and Darwinism by Wallace (1890). Ever since, the debate has not lost its passion (Endler, 1986; Grafen, 1987; Andersson, 1994; Clutton-Brock, 2004; Lessells et al., 2006; Roughgarden et al., 2006; Carranza,
2009; Clutton-Brock, 2009; Shuker, 2010). Darwin himself addressed these difficulties by distinguishing between the effects of sexual selection from natural selection (Darwin, 1871, page 257; and see Box 1).

The evidence that females also have a say in advertising traits and in competition for mates has further complicated the view of the classic Darwinian mechanisms operating on sexual selection, namely male-male competition and female choice (Darwin, 1871). As pointed out by Clutton-Brock (2009), females may be subject to selection similar to that operating on males under various ecological conditions, such as a female-biased operational sex ratio that generally promotes reversing sex roles either fully or partly (Vincent et al., 1992; Vepsalainen and Savolainen, 1995; Butchart, 2000).

Besides its central role in reviving the field of sexual selection, the natural/sexual/social selection debate is important for understanding how repeated patterns in evolution arose in light of the variable selection pressures. The evolution of female ornaments is one biological pattern that is currently at the crux of the discussion, although similar traits in males are generally accepted and are attributed to sexual selection (for review, see Clutton-Brock, 2007, Clutton-Brock, 2009).

Here, we discuss the possible selection types operating on female moth pheromones as a sexually dimorphic secondary trait. In doing so, we adopt the suggestions of Shuker (2010) and Tobias et al. (2012) to categorize the operating selection pressure based on the type of resources the organisms are competing for. Competition over mates is attributed to sexual selection (Darwin, 1871; Andersson, 1994; Shuker, 2010). Competition for ecological resources other than mates is attributed to social selection (Tobias et al., 2012), and obtaining a mate of the right species (Dobzhansky, 1937), is attributed to natural selection. These three types of selection are not mutually exclusive. On the contrary, they may all contribute to the shaping of female pheromones in relation to the various ecological contexts. In all selection types, the fitness coin by which the success of the individuals is determined is the number or quality of offspring they leave (Box 1, Table 1).

1 Female Sex Pheromones and Natural Selection

Pheromones may have evolved by natural selection when no benefit is expected by choosing a particular conspecific mate (i.e., absence of mate choice). Dobzhansky (1937) postulated that natural selection acts against hybrids through adaptive behavioral changes and sexual traits. As such, traits that avoid interspecific mismatched matings are shaped by natural selection because males and females of the same species have a mutual interest in nullifying the risk of producing no or infertile hybrid offspring (Paterson, 1985; Löfstedt et al., 1991; Baker, 2002; Mas and Jallon, 2005). Accordingly, sex pheromones are expected to be under strong stabilizing selection to prevent changes in the exact signal because slight deviations from the species code may lead to interspecific mating.

Evidence for natural selection operating on species-specific sex pheromones is scarce but does exist. As a product of natural selection, differences in phero-

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**Box 1 Definitions**

Darwin (1871) distinguished between two selection types that promote the evolution of phenotypic traits: (1) natural selection, which acts on characters that involve the "struggle for existence", and (2) sexual selection, which acts on characters in relation to competition for mates.

West-Eberhard (1983) introduced a third type of selection (3), social selection, which acts on traits that promote the competition among conspecífics over resources that are not directly associated with mates.

According to these definitions, sexual selection acts in the context of mate choice and competition over mates, social selection contributes to the evolution of traits in the context of competition for resources other than mates, and natural selection affects characters that involve solitary individuals or individuals in the solitary phase of their life cycle and traits that are not directly affected by competition with conspecifics.

In the context of evolution of female sex pheromones, natural selection shapes the pheromone for species recognition (it stabilizes selection), sexual selection promotes differences in pheromone blend (mainly in the amount and ratio of components) among conspecific females, and social selection affects female perception (auto-detection) of the pheromone and behavior that increases reproductive success in the presence of competing females.

The selection types are not mutually exclusive and may act simultaneously, reflecting pheromone plasticity in response to ecological constraints, resulting in pheromone plasticity in relation to ecological constraints. For example, the female sex pheromone of *Heliothis virescens* may change when the moth is sympatric with a closely related species (Groot et al., 2005), thereby responding to the pressures of natural selection. At the same time, the pheromone is costly to produce (Foster and Johnson, 2010) and thus can serve as an honest signal of female size and age, thereby responding to sexual selection.
mone characteristics in related sympatric species, such as those sharing geographical zones or the same host species, are expected. In bark beetles, the most pronounced differences in the pheromone blends have been found among the most closely related beetles in each genus (Symonds and Elgar, 2004). Similarly, species from species-rich moth families tend to have more components in their female-released pheromone blend than do species from species-poor families, allowing for a larger number of unique blends (Byers, 2006). It is useful to consider species that occur in allopatric and sympatric populations with close relatives. For example, females of the sheep moth *Choristoneura fumiferana* and *H. subflexa* in allopatry produce the same active compound in their sex pheromone blend (acetate ester). When these species are sympatric, pronounced differences in the pheromone blends have been found among the most closely related beetles in each genus (Symonds and Elgar, 2004). Indeed, females of the European corn borer 

Table 1  Examples of selection type, the affected trait, and the fitness gained

<table>
<thead>
<tr>
<th>Selection type</th>
<th>Species</th>
<th>Character</th>
<th>Fitness component</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural</td>
<td>Bark beetles</td>
<td>Pheromone plasticity</td>
<td>Avoidance of hybrids</td>
<td>Symonds and Elgar, 2004</td>
</tr>
<tr>
<td>Natural</td>
<td><em>Hemileuca eglanterina</em> (Lepidoptera)</td>
<td>Pheromone plasticity</td>
<td>Avoidance of hybrids</td>
<td>Mcelfresh and Millar, 2001</td>
</tr>
<tr>
<td>Natural</td>
<td><em>Lobesia botrana</em> (Lepidoptera)</td>
<td>Pheromone plasticity</td>
<td>Avoidance of hybrids</td>
<td>Gries et al., 2001</td>
</tr>
<tr>
<td>Natural</td>
<td><em>Heliothis virescens</em> (Lepidoptera)</td>
<td>Pheromone plasticity</td>
<td>Avoidance of hybrids</td>
<td>Groot et al., 2005</td>
</tr>
<tr>
<td>Natural</td>
<td><em>Drosophila serrata</em> (Diptera)</td>
<td>Pheromone plasticity</td>
<td>Avoidance of hybrids</td>
<td>Higgie et al., 2000</td>
</tr>
<tr>
<td>Sexual</td>
<td><em>Lobesia botrana</em> (Lepidoptera)</td>
<td>Pheromone characteristics</td>
<td>Honest advertisement</td>
<td>Harari et al., 2011</td>
</tr>
<tr>
<td>Sexual</td>
<td><em>Neoleucinodes elegantalis</em> (Lepidoptera)</td>
<td>Pheromone characteristics</td>
<td>Honest advertisement</td>
<td>Jaffe et al., 2007</td>
</tr>
<tr>
<td>Sexual</td>
<td><em>Mamestra brassicae</em> (Lepidoptera)</td>
<td>Pheromone characteristics</td>
<td>Honest advertisement</td>
<td>Noldus and Potting, 1990</td>
</tr>
<tr>
<td>Sexual</td>
<td><em>Heliothis zea</em> (Lepidoptera)</td>
<td>Pheromone characteristics</td>
<td>Honest advertisement</td>
<td>Raina et al., 1986</td>
</tr>
<tr>
<td>Sexual</td>
<td><em>Choristoneura fumiferana</em> (Lepidoptera)</td>
<td>Calling behavior</td>
<td>Competition for mates</td>
<td>Palaniswamy and Seabrook, 1985</td>
</tr>
<tr>
<td>Sexual</td>
<td><em>Adoxophyes Sp</em> (Lepidoptera)</td>
<td>Calling behavior</td>
<td>Competition for mates</td>
<td>Noguchi and Tamaki, 1985</td>
</tr>
<tr>
<td>Sexual</td>
<td><em>Homona magnanima</em> (Lepidoptera)</td>
<td>Calling behavior</td>
<td>Competition for mates</td>
<td>Noguchi and Tamaki, 1985</td>
</tr>
<tr>
<td>Social</td>
<td><em>Choristoneura fumiferana</em> (Lepidoptera)</td>
<td>Egg laying</td>
<td>Competition for resources</td>
<td>Palaniswamy and Seabrook, 1978</td>
</tr>
<tr>
<td>Social</td>
<td><em>Choristoneura rosaceana</em> (Lepidoptera)</td>
<td>Egg laying</td>
<td>Competition for resources</td>
<td>Goeke et al., 2007</td>
</tr>
<tr>
<td>Social</td>
<td><em>Lobesia botrana</em> (Lepidoptera)</td>
<td>Egg laying</td>
<td>Competition for resources</td>
<td>Harari et al., 2011</td>
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sent (in Bohemia, the Czech Republic) (Gries et al., 2001). In their influential studies, Groot and her colleagues (2005; 2006; 2007; 2009) found temporal variation in the pheromone blend of *Heliothis virescens* and *H. subflexa*, suggesting that the pheromone composition may be altered based on the female experience concerning the risk of mating mistakes in sympatric populations and the risk of sexual harassment by *Helicoverpa zea* males.

An additional mechanism that may have evolved to reduce interspecific matings is the development of specific chemical receptors that have higher affinity to components in the pheromone of a sympatric sister species. Adding these components to the otherwise typical species-specific sex pheromone often reduces male attraction to the female (Löfstedt, 1990; Löfstedt et al., 1990).

Phelan and Baker (1987) supported the view that sex pheromones have an adaptive role in preventing mating mistakes. They demonstrated that pheromone-releasing organs in males are more common in closely related species, sharing the same host, than in species in distinct populations. Tortricid moths, for example, lack pheromone-emitting organs, and only a small portion of this moth family shows host overlap.

When functioning to prevent mistakes in mating, sex pheromones are expected to be under stabilizing selection (Löfstedt, 1993; Linn and Roelofs, 1995; Butlin and Trickett, 1997; Phelan, 1997; Zhu et al., 1997; Shaw and Parsons, 2002). Indeed, females of the European corn
borer moth Ostrinia nubilalis produce two types of sex pheromone blends that differ only in the ratio of the two major components (Linn et al., 1997). As a result, males of one population are less attractive to females in the other population (Liu and Haynes, 1994; Linn et al., 1997; Zhu et al., 1997). Restricted male response to a change in a female pheromone blend was also demonstrated in other species (Löfstedt, 1990; Linn and Roelofs, 1995; Zhu et al., 1997). These findings, however, are in contrast with other studies that demonstrate individual variation in female sex pheromones in a population, both in the quantity and the ratio of components (Collins and Cardé, 1985; Witzgall and Frérot, 1989; Löfstedt, 1990; Jaffe et al., 2007; Harari et al., 2011). Furthermore, contrary to the prediction evoked by natural selection, males often respond to a wide array of the sex-specific pheromone blends (Löfstedt, 1990; Linn and Roelofs, 1995; Roelofs et al., 2002).

The latter findings, which counter the view that sex pheromones are highly conserved, have led to the inference that changes in pheromone characteristics (within an individual life time and at the population level) can influence mate choice. Hence, the concept of sex pheromones as a secondary trait that is shaped by sexual selection has been increasingly considered (Johansson and Jones, 2007).

2 Female Sex Pheromones and Sexual Selection

According to the broad definition of sexual selection (Andersson, 1994; Shuker, 2010; Tobias et al., 2012), a sexually selected trait is one that influences intraspecific competition for mates. This includes competition for the number or quality of mates and for resources that directly influence the probability of mating. Although the role of chemical signals in sexual selection was first suggested by Darwin (1871) (Box 1), sex pheromones were not often recognized as traits that affect competition for mates. In his book *Sexual Selection*, Andersson (1994) cited less than a handful studies on pheromone-mediated mate choice. Similarly, in their review of the various ecological, behavioral, and biochemical aspects of hydrocarbons in insects, Howard and Blomquist (2005) did not consider the role of hydrocarbons in sexual selection.

More recently, Johansson and Jones (2007) have addressed the challenge to review the rapidly increasing number of studies concerning the role of sexual selection in shaping sex pheromones (Johansson and Jones, 2007, Page 265). They categorized sex pheromones according to their part in mate choice with respect to species recognition, mate recognition, and mate assessment. The first two categories, choice of the correct species and mating status, do not take part in the competition for mates per se, and we have discussed them in the current review as part of natural selection (see above). Regarding pheromone-based mate assessment, Table 2 in Johansson and Jones (2007) lists 21 species in which males advertise their quality (fluctuating asymmetry, major histocompatibility complex, immunocompetence, competitive ability, attractiveness) but only two species in which females signal their condition (age and size) through sex-specific pheromones: the copepod Tigriopus japonicus (Ting et al., 2000), and the snake Thamnophis sirtalis (Lemaster and Mason, 2002).

Johansson and Jones (2007) attribute the dearth of studies demonstrating the use of sex pheromones as advertising traits by female moths to the minute amount of sex pheromone typically released (El-Sayed, 2010) and its low cost of production (Cardé and Baker, 1984; Kokko and Wong, 2007), thus, "...seems an unlikely result if they were subject to mate choice" (Johansson and Jones, 2007, page 257). Johansson and Jones agree with the general view that females signal to males when the cost of advertising is low, while males signal to females when the cost of advertising is high (Greenfield, 1981; Svensson, 1996; Landolt and Phillips, 1997; Johansson and Jones, 2007). According to this line of reasoning, female sex pheromones cannot serve as secondary, extravagant traits that reveal female quality because a substantial cost of the trait or of its maintenance is a prerequisite of honest advertising (Zahavi, 1977; Kotiaho, 2000, 2001, 2002).

In general, the elaborate traits of females have attracted considerably less research attention than those of males (Amundsen, 2000), although the females of many species do have such traits (Andersson, 1994; Clutton-Brock, 2004; Kraaijeveld et al., 2007). The origin of this research bias lays at the feet of Darwin, who suggested that female secondary traits are derived from the showy secondary traits of males (Darwin, 1871; Lande, 1980). In the last decade, accumulating research has demonstrated that, like the ornaments of males, those of females may have been selected by female-female competition over mates and by male choice of females, i.e., by sexual selection (see examples in Clutton-Brock, 2007, 2009; Rosvall, 2011; Tobias et al., 2012).

Competition among females for mates is expected when male quality varies and when the operational sex
ratio is female-biased. Evidence from non-pheromone signals is plentiful (see Rosvall, 2011). In the case of the deep-snouted pipefish *Syngnathus typhle*, for example, females compete for mates, displaying their ornamentation to establish a dominance hierarchy, and males consider the female hierarchy when choosing their mates (Berglund and Rosenqvist, 2001). Similarly, female age in the pinyon jay *Gymnorhinus cyanoccephalus* is correlated with malar and head coloration, which are used to assess dominance in female competition for mates (Johnson, 1988).

Accepting that sex pheromones function as secondary traits subject to sexual selection (Darwin, 1871; Andersson, 1994; Shuker, 2010), one can make three predictions. First, females vary in the trait under selection (i.e., the emitted pheromone). Second, females compete for mates, advertising their quality via the sex pheromone. Third, males are influenced by the message conveyed through the pheromone. Concerning the first prediction, individual variation in pheromone characteristics (i.e., the amount and ratio of components) has been documented for several insect species (e.g., for bark beetles: Birgersson et al., 1988; and for moths: Miller and Roelofs, 1980; Haynes et al., 1984; Safonkin and Bykov, 2006). The variations may include the overall amount of the pheromone and/or a different ratio of the components in the pheromone blend (Collins and Cardé, 1985; Witzgall and Frérot, 1989; Löfstedt, 1990; Svensson et al., 1997; Jaffe et al., 2007; Harari et al., 2011).

Concerning the second prediction, there is evidence that female moths use female sex pheromones to compete for mates. For example, females increased calling behavior when they sensed pheromones released by conspecific females (Palaniswamy and Seabrook, 1985; Stelinski et al., 2006). These females may be attempting to attract early mate-searching males. Females of other moth species delay calling when exposed to conspecific pheromone (Noguchi and Tamaki, 1985; Weissling and Knight, 1996). These and other examples suggest that female calling alters the calling of other conspecific females and that such changes may affect future reproductive success (Goekce et al., 2007; Yang et al., 2009).

As is the case for other extravagant traits (Zahavi, 1977), female sex pheromones are expected to honestly reveal the signaler’s physiological state through rapid changes in the quality and quantity of their pheromone (Alimiazee and Stafford, 1971; Webster and Cardé, 1982; Liu and Haynes, 1994). Thus, the signal should allow males to discriminate among females for reproduction (as suggested by Atema 1986 and demonstrated by Jaffé et al. 2007 and Harari et al. 2011). That pheromones advertise female quality is often demonstrated by quantifying the cost of advertising (Foster and Johnson, 2011; Harari et al., 2011). Quantity and ratio of components in the female moth sex pheromone may reveal female size (Jaffé et al., 2007; Harari et al., 2011) and age (Miller and Roelofs, 1980; Raina et al., 1986; Noldus and Potting, 1990). Cost of pheromone production was behaviorally demonstrated, i.e., mortality rates were higher and fecundity was lower for females that released pheromones than for those that did not (Foster, 2009; Harari et al., 2011). There is also evidence that females investing in resistance to insecticides produce reduced amounts of pheromones (Campanhola et al., 1991; Delisle and Vincent, 2002), indicating a high metabolic cost of pheromone production (Foster, 2005, 2009; Foster and Johnson, 2010).

Female advertising and male mate choice are predicted when mating is costly for males (Zahavi, 1977; Kokko and Monaghan, 2001; Byrne and Rice, 2006), which is often associated with female phenotypic variation (Harari et al., 1999; Kvarnemo and Simmons, 1999; Jaffé et al., 2007; Harari et al., 2011) and female-biased sex ratios (Parker, 1983; Owens and Thompson, 1994; Johnstone et al., 1996). Mating cost for males may include energetic courtship displays (Segoli et al., 2006), presenting the females with nutritive nuptial gifts (Thorhill, 1980; Dewsbury, 1982), intense intrasexual competition for mates (Bonduriansky and Brooks, 1999; Fromhage and Schneider, 2005), and in the case of all moth species, limited sperm supply (Friedlander et al., 2005; Teng and Zhang, 2009).

In species in which females have multiple mates, sperm competition may affect the reproductive output of the males. If the pheromone signals the female reproductive state, males may allocate resources, increasing their reproductive potential accordingly. Males of the white widow spider, *Latrodectus pallidus*, for example, performed a significantly shorter display when approaching mated females because the risk of cannibalism is considerably reduced (Harari et al., 2009). Additionally, the amount of sperm that male moths transfer to females is correlated with female mating experience and age (Wedell and Cook, 1999; Teng and Zhang, 2009).

As opposed to males of most other taxa, male moths stop producing fertile sperm in the pupal stage (Friedlander et al., 2005). As a consequence, sperm reserves are diminished after each copulation, and the potential...
number of females that can be inseminated is limited (Callahan and Cascio, 1963; Friedlander et al., 2005; Teng and Zhang, 2009). In addition, females suffer reduced reproductive success after mating with experienced, polygynous males (Torres-Vila and Jennions, 2005; Lauwers and Van Dyck, 2006; Marcotte et al., 2006) and thus may discriminate against them. Indeed, males prefer larger, more fecund females (Torres-Vila et al., 2002), as indicated by the features of the pheromone emitted by the female (Jaffe et al., 2007; Foster and Johnson, 2011; Harari et al., 2011).

3 Female Sex Pheromones and Social Selection

The currently understood definitions of natural selection and sexual selection (Darwin, 1871; Andersson, 1994; Shuker, 2010) leave some behaviors in a grey area. Males and females may differ in their struggle for increased reproductive success. In general, males compete for access to females, while females compete for access to resources (Rubenstein, 2012; Tobias et al., 2012). Although both males and females often use ornaments to achieve higher fecundity, male extravagant traits are used to obtain mates directly (e.g., through male-male fighting) or indirectly (e.g., by defending territory), while females traits are often used to obtain resources other than mates (e.g., food patches and nest sites) that are needed for offspring welfare after competition over mates has ended successfully (Carranza, 2009; Clutton-Brock, 2009). Tobias et al. (2012) followed West-Eberhard (1983) in suggesting that intraspecific competition for resources other than mates represents a different form of selection that they termed social selection. In this context, signaling traits (e.g., ornaments, weapons, elaborate displays) may be involved in direct or indirect competition for resources other than mates or used in non-sexual contests (Moore et al., 1997; Wolf et al., 1999; Mcglothlin et al., 2010; Rosvall, 2011) and yet still provide relevant information about the signaler.

One such example of a socially selected trait is the horn of the female dung beetle. The female dung beetle uses its horn in intrasexual competition for breeding resources (Watson and Simmons, 2010) which affects the number and quality of surviving offspring. Another example may include competition by tropical streak-backed orioles for foraging territory during breeding and non-breeding seasons (Murphy et al., 2009). Females may also benefit from aggressive behavior toward conspecific females when breeding opportunities are costly to find. Females of the common goby Pomatoschistus microps, for example, exhibit antagonistic behavior at sites with a shortage of nests (Borg et al., 2002), and only winners of aggressive interactions between individuals of the parasitoid Pachycrepoides vindemmiae gain access to oviposition sites (Goubault et al., 2007).

Like morphological and behavioural traits, sex pheromones may play a role in intrasexual competition over breeding resources. Females can detect their airborne species specific pheromone (Palanaswamy and Seabrook, 1978; Noguchi and Tamaki, 1985; Goekce et al., 2007). There is evidence that the release of pheromone by females affects the oviposition of conspecific females. Exposure of the female to the sex pheromone of its own species stimulates oviposition for some moth species, e.g., Choristoneura fumiferana; (Palanaswamy and Seabrook, 1978) but deters oviposition by other moth species (Palanaswamy and Seabrook, 1978; Goekce et al., 2007; Harari et al., 2011). In both cases, mated females compete for oviposition sites. The airborne pheromone released by the female provides information about the signaler’s physical condition (Jaffe et al., 2007; Foster, 2009; Harari et al., 2011) and thus provides information about the forthcoming intensity of offspring competition for food. This behavior is similar to female competition at time of pregnancy or maternal care (Wolff and Peterson, 1998; Rodel et al., 2008).

4 Summary

Substantial evidence indicates that sex pheromones in general and female-produced sex pheromones in particular function as secondary (signaling) traits. The nature of the selection acting on the female trait should be defined in terms of the resource being competed for. The definition of the operative selection pressure is not simply semantic but is relevant to the trait’s potential adaptive (or non-adaptive) significance. As demonstrated in this review, the female sex pheromone is an adaptive trait that is moulded by three selection pressures: natural, sexual, and social selection. Natural selection acts on species recognition and reduces the probability of mismatched matings. Sexual selection acts through female intraspecific competition for mates and male choice of females (although mutual choice is also possible because females still heavily invest in the offspring). In social selection, females use the trait to compete against conspecific females for ecological resources. The contribution of social selection to evolution of the female sex pheromone as a signaling trait is
difficult to assess because the evolution of pheromones has been traditionally attributed to either natural selection or sexual selection. However, recent papers demonstrate that female moths use sex pheromones to advertise their reproductive potential, and that males use this information when choosing females as mates. Thus, it is not unreasonable to hypothesize that female sex pheromones provide information about the intensity of the impending competition among offspring for essential resources. There is growing evidence that females can detect airborne, species-specific pheromone produced by conspecific females and use the information to compete for resources or take flight in a search for resources elsewhere.

It is interesting and perhaps initially perplexing that the exact same trait, the female sex pheromone, may be subjected to three different selection pressures. Moreover, the selection pressures are expected to have different effects on pheromone variance, i.e., natural selection should reduce variance (stabilizing effect) but sexual and social selection should enhance variance. Given the importance of the trait in preventing the production of unfit hybrid offspring and in mediating sexual and social communication, plasticity in the female sex pheromone presumably enables its adjustment in response to various environmental and competitive constraints. An excellent example of such plasticity is provided by Heliothis virescens (see Box 1). Females of this moth species can change their sex pheromone to reduce the risk of incorrect mating (Groot et al., 2005) and can also apparently use their sex pheromone as an honest signal of female size and age (Foster and Johnson, 2010). Whether such plasticity in the female sex pheromone is common among moths and other species warrants additional research.

References


