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When sexual signallers are choosers too

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1 | General introduction

Naomi L. Zweerus

Sexual selection is a potent evolutionary force

Sexual selection is a strong evolutionary force and comprises any selection that results from fitness differences associated with non-random mating success (reviewed in Shuker & Kvarnemo, 2021). The concept of sexual selection was proposed by Darwin because the evolution of exaggerated sexual ornaments, like the peacocks' tail and the long tails of male widowbirds (Andersson, 1982, 1994), could not be explained by natural selection alone (Darwin, 1871). Only a preference and thus selection for such extreme sexual signals can explain their evolution (Fisher, 1930; Majerus, 1986). However, it is not only selection for extremes but also the selection for intermediate trait values that can impact signal evolution. If the risk of hybridization between populations with similar sexual signals is high, the average signal of the population should be preferred. Stabilizing selection drives populations towards a mean trait value and increases the difference between populations with similar sexual signals. This results in divergence of sexual signals which may cause reproductive isolation between populations. Closely related species indeed often differ strongly in their sexual traits, suggesting that sexual selection may drive speciation (Price, 1998; Ritchie, 2007). Two main mechanisms underlie this potent evolutionary force: competition and mate choice.

The two mechanisms of sexual selection**Competition (within sexes)**

Individuals of the same sex may compete for partners. Male traits involved in competition that have evolved into elaborate ornaments provide some popular examples of sexual selection. Examples of these traits can be found in the antlers of male deer, the horns of beetles, or the proboscis of male elephant seals. Winners of inter-male competition obtain access to fertile females and thus can reproduce (Andersson, 1994). While combat between males for access to females (contest competition) is probably the most illustrative example, competition can also relate to locating prospective mates fastest (scramble competition) and/or to enduring prolonged reproductive activity (endurance rivalry) (Andersson, 1994; Shuker & Kvarnemo, 2021). Selection for traits occurs whenever they confer a competitive advantage.

Mate choice (between sexes)

When potential partners vary in quality, mating investment is high, and/or there is a chance of attracting alternative partners, individuals can benefit from selecting mating partners (Parker, 1983; Kokko & Johnstone, 2002). These benefits may affect immediate reproductive success (direct benefits), for instance by influencing access to territories, resources, or parental care (Andersson, 1994), or the genetic quality of offspring (indirect benefits) (Fisher, 1930; Møller & Jennions, 2001; Kokko et al., 2003; Andersson & Simmons, 2006). In general, mate choice is the "process that occurs whenever the effects of traits expressed in one sex leads to non-random allocation of reproductive investment with members of the opposite sex" (Edward, 2015). The expressed traits are sexual signals and provide information about the sender. Signals underlying mate choice can be behavioural, morphological, or physiological traits (or a combination thereof) that comprise an individual's attractiveness to the opposite sex. Attractive signals can indicate good quality of the sender (sometimes referred to as honest signals (Zahavi, 1977; Grafen, 1990;

Johnstone, 1995)). Variation in quality, related to genetic quality and/or physiological condition, therefore leads to variation in sexual signals and allows receivers of the signal to differentially assess partners.

Two signallers and two choosers

Communication is key to the process of selection by mate choice; the chosen sex signals to the choosing sex, who responds to the sexual advertisement in discriminative manner. The conventional perspective on mate choice is that one sex signals while the other sex responds. However, males and females within a species can both be reciprocal signallers and responders. Thus, both sexes send sexual signals and both sexes choose partners. Such mutual mate choice can be expected when both sexes invest in mating and show similar variance in reproductive success (Trivers, 1972), and when both sexes vary in quality (Parker, 1983; Johnstone et al., 1996; Bergstrom & Real, 2000). Mate choice by both sexes has been mostly recognised in birds (Kraaijeveld et al., 2007) and is most often observed in mating systems with biparental care (e.g., Zebra finches *Poephilia guttata* (Burley, 1986)), but might be more common than originally thought (e.g., Bonduriansky, 2001; Cotton et al., 2006; Edward & Chapman, 2011; Rosenthal, 2017). When males and females are mutual choosers, selection by both sexes can significantly increase the number and interactions of selective forces on sexual signals.

Mutual mate choice can be on the same type or on different types of signals

If males and females are reciprocal signallers, their signals can be the same type or different types of signals. The same types of signals have the same sensory modality and share an underlying biosynthetic pathway. Mutual mate choice on the same type of signal has been found in birds (Kraaijeveld et al., 2007), where both sexes may select partners based on plumage colouration (Amundsen et al., 1997), crests (Jones & Hunter, 1993, 1999), or sexually monomorphic songs (Langmore, 1998). Some insects also produce monomorphic acoustic signals to attract partners (Henry et al., 2002, 2013).

Different types of sexual signals operate via different sensory modalities, do not share an underlying biosynthetic pathway and/or are produced by different tissues. For instance, female mantids attract males from a distance using sex pheromones (Hurd et al., 2004; Holwell et al., 2007; Maxwell et al., 2010; Mahmudunnabi & Barry, 2019), while males rely on visual cues for mate choice (Roeder, 1935; Edmunds, 1975; Maxwell, 1999; Barry et al., 2015). Evidence is also accumulating to show that birds may use different signal types for mate choice. For example, male ducks impress with their colourful plumage while several lines of evidence show that females emit chemical signals, although their function as sexual signals is controversial (Wyatt, 2003; Caro & Balthazart, 2010). Signals that are derived through different biosynthetic pathways have been found in chemical signals. For example, in arctiid moths, females synthesise a sex pheromone in a pheromone gland or in specialised cells (oenocytes) (Conner et al., 1980; Bendib & Minet, 1998), while males produce a different sex pheromone consisting of derivatives of ingested secondary plant metabolites (Nishida, 2002; Henneken et al., 2017).

Evolutionary consequences of mutual mate choice depend on whether the choice is based on the same or different signals

When mutual mate choice is based on the same signal, then selection pressure operates from (at least) two sides. Sexual selection theory predicts stabilizing selection for traits used in species recognition, whereas directional selection can be expected for traits that are used to assess mate quality (Fisher, 1930; Johansson & Jones, 2007). Mutual mate choice may thus lead to both directional and stabilizing selection when acting on the same type of sexual signal produced by both sexes and interaction effects may occur. However, mutual mate choice may also target different traits in which case the evolution of each signal needs to be considered separately. Female and male sexual signals and preferences may evolve independently depending on whether the traits are correlated, either biosynthetically and/or genetically (Kirkpatrick & Hall, 2004; Sæther et al., 2007). To identify the direction and strength of sexual selection on sexual signals, it is necessary to determine a) whether there is mutual mate choice, and b) whether the same or different types of signals are used by each sex for mate choice.

Sexual signals can be under sexual and natural selection

Sexual and natural selection are not mutually exclusive. While sexually selected traits create a mating advantage, they can have a survival disadvantage. Hence, natural selection will affect the elaboration of these traits, as elaboration is associated with costs. Costs can be related to higher resource investment for developing the trait (e.g., bigger size (e.g. Chown & Gaston, 2010) or more intense colouration (e.g., Hill, 1996; Kodric-Brown, 1998)) but also increased mortality. Predation risk may increase because predators use the signal to locate the prey and parasitoids may follow the hosts' sexual signal (e.g., Zuk & Kolluru, 1998; Rosenthal et al., 2001; Woods et al., 2007; Johnson & Candolin, 2017). In the example of male widowbirds, the long tails come at a cost, as they require resources to develop and make it harder for males to fly (Andersson, 1994). However, such costly ornaments can indicate quality and are therefore sexually selected (Zahavi, 1975). These signals evolve under opposing selection pressures of natural and sexual selection.

A scenario where natural and sexual selection act in concert is when pre-existing sensory systems become attuned to sexual signals (sensory bias). For example, if a female preference initially developed in the context of food preference, while the male traits that developed later are attuned to the same stimulus (reviewed in Andersson & Simmons, 2006). In this case, natural selection precedes sexual selection. Depending on the context, natural and sexual selection pressures may act in the same or opposite direction and ultimately shape sexual communication.

Sexual communication in moths is relevant for species recognition

Moths are famous for their chemical sexual communication and are among the most diverse group of animals with about 120.000 species identified (Bazin et al., 2013). Every species has its own sexual communication channel. Sexual communication of moths has been well studied but mostly in terms of species-specific long-range female sex pheromone blends to attract males (Vickers & Baker, 1997; Baker & Vickers, 1997; Wyatt, 2003; Cardé & Haynes, 2004; El-Sayed, 2011). Females emit a sex pheromone from an everted ovipositor in a behaviour termed 'calling'

(Gaston & Shorey, 1964; Gentry et al., 1964; Tumlinson et al., 1975; McNeil, 1991; Wedell, 2005). Males navigate to conspecific females in a characteristic zig-zag flight (Baker, 1986; Vickers & Baker, 1997; Vickers, 2002). Mate choice for species recognition is a crucial and well-studied aspect in species where mate signals overlap between closely related species (Löfstedt, 1993; Price, 1998; Cardé & Haynes, 2004; Symonds & Elgar, 2008). Since hybrids are sterile (Harrison & Doncaster, 1914; Pair et al., 1977; Laster, 1972; Laster & Hardee, 1995; Wang & Dong, 2001), errors in species-recognition are selected against. The mean signal is preferred to minimize interspecific attraction, which leads to stabilizing selection (Paterson, 1985; Löfstedt, 1993; Linn et al., 1997; Zhu et al., 1997; Droney et al., 2012). However, stabilizing selection cannot explain the high diversity of sexual signals in moths (Greenfield, 1981; Löfstedt, 1993; Symonds & Elgar, 2008).

Moth sexual communication includes long-range females signals and short-range male signals

A central paradox in evolutionary biology is how within-species variation in sexual signals is maintained when strong stabilizing selection should deplete variation in these traits. Different selection pressures than those which are generally assumed must be the reason that intraspecific variation in these traits is maintained (De Pasqual et al., 2021). So far, our understanding of sexual selection pressures on moth sexual signals has been predominantly based on the male preference for the female sex pheromone. Despite the fact that males of many moths possess elaborate scent structures (androconia or hairpencils) and emit volatiles at close range (Grant, 1970; Teal & Tumlinson, 1989; Birch et al., 1990), female mate choice in moths has been neglected (but see Iyengar & Eisner, 1999). If both sexes execute mate choice, selection pressures may be fundamentally different than when only one sex chooses. Male and female behaviours combined might explain how variation is maintained, because mutual mate choice is likely to result in selection pressures that can maintain variation (Jennions & Petrie, 1997; Pryke & Griffith, 2007). Establishing the existence of female mate choice and deciphering the effect of selection by female mate choice, and eventually mutual mate choice, is thus the first step to a better understanding of sexual signal evolution. We can hypothesize that by shifting the focus to female mate choice and male sexual signals (i.e., the male hairpencil pheromone), we can unravel how intraspecific variation in sexual signals can be maintained.

Are both sexes of the tobacco budworm *Chloridea (Heliothis) virescens* (Fabricius, 1777) signallers and responders?

Chemical sexual communication of the tobacco budworm *Chloridea (Heliothis) virescens* (Lepidoptera: Noctuidae) has been extensively studied, with a focus on the female sex pheromone. Females emit a species-specific pheromone blend to attract males (Löfstedt, 1993; Cardé & Haynes, 2004) (Fig. 1). Both males and females mate only once a night, but several times over multiple nights (Flint & Kressin, 1968; Raulston et al., 1975; Pair et al., 1977; Gao et al., 2020). This polygamous mating pattern benefits both sexes as offspring number increases with multiple matings (Gao et al., 2020). During mating, which generally lasts 2-3 hours (Pair et al., 1977; Blanco et al., 2009; Hosseini et al., 2016), the male ejaculate transforms into a spermatophore (LaMunyon, 2000; Blanco et al., 2009). A spermatophore can weigh up to 5% of

the male's body weight (LaMunyon, 2000; Blanco et al., 2009). When females mate with different males, sperm from various males fertilizes eggs (LaMunyon & Eisner, 1993; LaMunyon, 2000; Blanco et al., 2008).

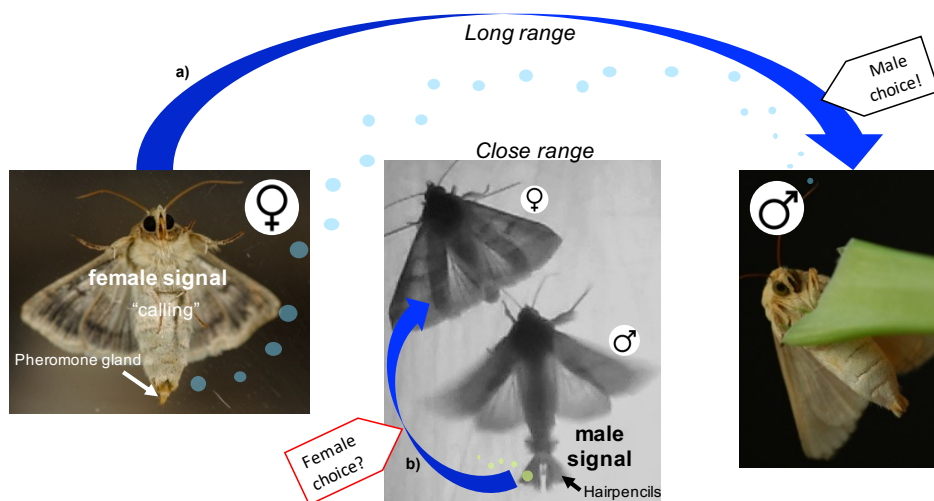


Fig. 1. Sexual communication in the tobacco budworm *C. virescens* depicted as a) female sex pheromone as a long-range attractant and b) male short-range signals during courtship. (Foto credits: Jan van Arkel, Naomi L. Zweerus)

Attracted males extrude their hairpencils upon arrival and emit a pheromone that is biosynthetically related to the female sex pheromone (Hendricks & Shaver, 1975; Teal et al., 1981; Teal & Tumlinson, 1989) (Fig. 1). Males perfume females with pheromone during copulation, which has anti-aphrodisiac effects on other males (Hosseini et al., 2016). Like males, females use the male hairpencil pheromone for species recognition (Hillier & Vickers, 2004). Whether these chemicals are also involved in female mate choice is unknown (Teal et al., 1981; Birch & Hefetz, 1987; Hillier & Vickers, 2004), and empirical support is, as yet, lacking. The main aim of this thesis was thus to determine if *C. virescens* females choose males and if so, to investigate the male signal underlying female mate choice.

Outline of the thesis

In chapter 2, I investigated whether female mate choice in *C. virescens* exists, and to what extent the male hairpencil pheromone affects female mating decisions. The study is to our knowledge the first comprehensive study on female mate choice in noctuid moths, and provides empirical evidence that also 'the other sex' (i.e., females) assess and discriminate among courters.

In chapter 3, I tested the extent to which female mating status affects female sexual behaviour and mate choice, in a species in which females are not only choosers but also signallers. By signalling, females can adjust the arrival rate of males and thus signalling increase the female's chance of mating. Theory predicts that non-signalling virgin females should not be choosy because the risk of remaining unmated is high, signalling virgins may be choosy since they can

actively attract males. I evaluated these predictions from theory on non-signalling females in signalling females.

In chapter 4, I deciphered if two newly described, nutrition-derived compounds of the *C. virescens* male hairpencil pheromone could underlie female mate choice. Males sequester these secondary metabolites after ingestion in the larval and adult stage. Since the amount of methyl salicylate (MeSA) and δ -decalactone (decalactone) both correlated positively with male pupal mass, I tested the hypothesis that female preference for larger males would result in more choices for males with higher amount of MeSA and/or decalactone.

In chapter 5, I looked at the chemical compounds on male and female legs of three closely-related moth species, and sought to identify the biological role of pheromone on moth legs. Since I determined tactile interactions during courtship (see chapter 2), I recognized a potential for alternative chemical communication. Furthermore, I explored whether the pheromone compounds on legs act as oviposition-detering signals, which does not seem to be the case. I then tested these chemicals for antimicrobial properties as an alternative function of pheromone compounds.

In chapter 6, I discuss the findings in relation to the main aim of the thesis and in a broader scientific context.

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