



Review

The trap of sex in social insects: From the female to the male perspective



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ABSTRACT

The phenotype of male Hymenoptera and the peculiar role of males has been neglected and greatly understudied, given the spectacular cooperative behavior of female social insects. In social insects there has been considerable progress in understanding the molecular mechanisms behind haplodiploid sex determination but, beyond that, very little is known concerning the neural, endocrine, and genetic correlates of sexual selection in males. An opportunity is being missed: the male phenotype in Hymenoptera is a natural experiment to compare the drives of natural versus sexual selection. In contrast to females, males do not work, they usually display far from the nest to gain mates, compete among rivals in nuptial flights or for a symbolic territory at *leks*, and engage in direct or ritualized conflicts. By comparing the available data on male paper wasps with studies on other social Hymenoptera, we summarize what we currently know about the physical, hormonal, neural and behavioral traits in a model system appropriate to examine current paradigms on sexual selection. Here we review male behavior in social Hymenoptera beyond sex stereotypes: the subtle role of “drones” in the colony, the lack of armaments and ornaments, the explosive mating crowds, the “endurance” race, the cognitive bases of the “choosy” male and his immune defense. Social insect males are not just simple-minded mating machines, they are shaped, constrained and perhaps trapped by sexual selection.

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Contents

1. Are insects a good model to explore sex-dimorphism in behavior and brain?	519
2. The neglected drone: male social hymenopterans in the Darwinian scenario	520
3. Mating syndromes of social Hymenoptera	522
4. Male insects in neuro-endocrine research	522
4.1. Organizational and activational effects of hormones on sexual behavior	522
4.2. Male hymenopterans: a brain for just one season	523
5. A new model for cognitive and neuroendocrine adaptations under sexual selection: a focus on <i>Polistes dominula</i> males	525
5.1. The reproductive apparatus and immune defense, from a male perspective	525
5.2. Studying lekking behavior: not just “child’s play”	527
5.3. The smart male: from the field to the lab	529
6. Wider challenges	529
Acknowledgments	530
References	530

1. Are insects a good model to explore sex-dimorphism in behavior and brain?

The evolutionary tree is not a hierarchy. It is tempting for all of us to view animals with which we share a more recent common

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ancestor as being just like us. Baboons and even bluebirds can look and act an awful lot like people. A good deal of my own research is done with *insects*, and one of the reasons I like working with them rather than with vertebrates is that *is harder to see myself reflected in their behavior*.

Marlene Zuk, *Sexual Selections. What We Can and Can't Learn about Sex from Animals*, 2002, Introduction, p. 3.

The challenge of this review it is to describe what is known about the forces of sexual selection which have shaped mating behavior, morphology and neuro-endocrine system of males in social Hymenoptera: wasps, bees, ants; and also to provide a roadmap for future studies by highlighting key questions for future research. The male phenotype is like the dark side of the moon. However it represents a natural experiment that has been greatly undervalued, to compare the drives of natural versus sexual selection, parental versus mating efforts, and their associated neurogenomic mechanisms. In social Hymenoptera males and females represent two divergent morphs. The primary abode of females (queens and workers) is the colony, whereas mating – the focus and the final chapter of male life history – occurs mainly outside the nest. The male, devoid of the constraints imposed by caste specialization, may be viewed as the output of sexual selection.

In *The Descent of man, and Selection in relation to Sex* (Darwin, 1871), the actors of sexual selection are “ardent males and choosy females”, i.e. male–male fighting and female choice. The “wonderful horns” of male rhinoceros beetles fit into Darwin's *armaments* category. Other traits, both morphological and behavioral, evolved because the females preferred them, i.e. are *ornaments*: again, in certain Coleoptera, “the splendid metallic tints” and “stridulating organs” of males (Chapter XI, p. 422).

While competition among males for the rights to mate with a female seemed reasonable enough to Darwin's Victorian contemporaries, virtually none of them could swallow the idea that females—of any species, but especially the so-called dumb animals—could possibly do anything so complex as discriminating between males with slightly different plumage colors. [...] Largely because of the opposition to the idea of female choice, sexual selection as a theory lay dormant for several decades.

Marlene Zuk, *Sexual Selections. What We Can and Can't Learn about Sex from Animals*, 2002; Introduction, p.7.

Modern behavioral ecology has moved beyond the paralyzing view of “dumb animals”, with an increasing appreciation for the behavioral complexity and cognitive capacities of insects. Thus, in addition to an easier evasion of the risk of anthropomorphism, studies on insects have played a lead role in developing new insights in sexual selection (Table 1).

The brain is one of the most important sexual organs; indeed, most sexual selection mechanisms rely on sensory/neural/cognitive differences among potential partners or rivals. Neural plasticity and learning may be involved in mating tactics, from competition to mate choice, from advertisement displays to mate guarding and pair bonding, in birds (Keagy et al., 2012) as well as in insects (Dukas, 2006, 2008) and other taxa. Neural sex dimorphism – in human and non-human animals – is the obvious consequence of Darwin's assumption: “sexual selection has apparently acted on both the male and the female side, causing the two sexes of man to differ in body and mind” (Chapter XXI, p. 402). Brain sex differences involve developmental, ecological and taxonomic differences. “Not all sexually selected traits are conspicuous. However, and when a sex difference consists of an enhancement of cognitive and perceptual ability, disentangling the separate actions of natural and sexual selection is difficult” (Jacobs, 1996). Nevertheless, some of these differences might be best understood within the framework of sexual selection and, in particular, in social Hymenoptera.

While female castes are hot topics in neuroscience and genetic analysis, social hymenopteran males are seldom subjects of molecular and neural studies of behavior, being instead used to study sex determination, sperm competition, long-term sperm storage, with some exploratory studies on brain transcriptome expression (mostly in *Apis*: Collins et al., 2006; den Boer et al., 2009; Stürup et al., 2013; Zareie et al., 2013; Zayed et al., 2012). Excellent reviews on genetic and genomic analyses in insect societies do not consider the male role, as this is surely marginal in terms of colony division of labor (Smith et al., 2008). In contrast to males' lack of social behavior, the mating biology of male social hymenopterans involves cognitive abilities, is flexible and open to alternative tactics. Thus, hymenopteran traits have been the result of diverse selective forces – individual selection, kin selection, group selection, and sexual selection – acting across species and between males and females.

The main goals of this review are: (i) to identify the role of males in social Hymenoptera, in which a massive emergence of males turns into collective mating syndromes; (ii) to organize the scarce and scattered neuro-endocrine data on males in an updated theoretical scenario; and (iii) to provide an overview of behavior and physiology of male *Polistes dominula*, a suitable model organism to investigate the expression of sexually selected traits by means of modern neuro-endocrine and genomic approaches.

2. The neglected drone: male social hymenopterans in the Darwinian scenario

Eusociality, evolved in ants, bees, wasps and a few other taxa, is a rare form of complex social behavior characterized by cooperative brood care, reproductive castes (queens/kings and workers), and overlapping generations (Michener, 1969). In the Hymenoptera, these impressive feats of cooperation are entirely limited to the female sex. Social insects are descended from solitary-nesting ancestors where only females care for young (Davies and Gardner, 2014). Thus, in social as well in solitary species, females are involved in nesting and brood care, due to sex-specific expression of genes for parental behavior (West-Eberhard, 2003). Sexuals (males and gynes, i.e. virgin potential future queens) typically emerge at the peak of colony development (with some exceptions, Strassmann, 1981). Long-lived queens leave the colony and, after mating, will start a new colony, whereas males die after the nuptial season (but see Shik et al., 2013; Kureck et al., 2013 about longevity in male ants).

Males lack the anatomical and behavioral adaptations to be efficient workers, such as the sting (Starr, 1985) and hunting and foraging for brood provisions (West-Eberhard, 1975), with some exceptions (see the moderately developed pollen baskets in bumble bee males observed also by Darwin, a case of “cross-sexual transfer”, West-Eberhard, 2003). Not surprisingly, the sex ratio of the colony is usually female-biased, a fact that has been recognized as far back as Charles Butler's 1609, *The Feminine Monarchie, or the Historie of Bees*, the first English book about beekeeping. In a bee hive, the males are less than 5% of the total number of females (Wilson, 2007). As a rule, in colonies of eusocial insects, the investment in males is one third of that in future queens (Trivers and Hare, 1976). This asymmetry is the output of the reproductive conflict between the queen and the workers, which are more related to sisters than to brothers or sons due to haplodiploidy (Hamilton, 1972).

Sex is determined by multi-allelic sex-determining loci (SDL) which, depending on the species, can consist of a single locus (such as the gene complementary sex determination) or many loci (Beukeboom et al., 2007). Females arise from fertilized diploid eggs that are heterozygous at the SDL and males from unfertilized haploid eggs. Diploid males – homozygous at the SDL – are rare and

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