

The neglected gender: Biology of the male social bee

Symposium organized by Gudrun Koeniger and Boris Baer

Male interests in eusocial Hymenoptera: An inclusive fitness perspective

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Inclusive fitness theory (Hamilton, W. D., 1964, *J. Theor. Biol.* 7: 1-52) has revolutionised our understanding of insect societies, particularly reproductive behaviour. On the one hand, inclusive fitness theory has helped us to understand how reproductive division of labour can be selected for by favouring helping behaviour in which working individuals rear the offspring of close relatives, thereby indirectly passing on copies of their genes to future generations. On the other hand, the theory also predicted that there would be reproductive conflicts within non-clonal insect societies. This challenged the traditional view of an insect society as a cooperative entity entirely focused on rearing the queen's offspring. Trivers and Hare's (1976, *Science* 191: 249-263) study of ant sex ratios was the first to present direct evidence for such conflict, in this case between the queen and the workers collectively. The workers favour, and typically get, a more female-biased allocation ratio than the even ratio which is the optimum of the mother queen. However, the queen and the workers are only two of the many parties of interest within a hymenopteran society. The workers individually, young female larvae prior to differentiation into queen and worker morphs, and the males all have their own interests concerning colony reproduction, and these may differ from the interests of either the mother queen or the adult workers collectively. The interests of the males also depend on whether they are of the parental generation or the offspring generation. The interests of males are typically ignored because males are assumed to have little power (Beekman, M., Ratnieks, F. L. W. 2003. Power and reproduction in insect societies. *Philosophical Transactions of the Royal Society B* 258: 1741-1753) to influence the reproductive characteristics of insect societies because males are not involved with brood rearing. This is probably just as

well in terms of making predictions from inclusive fitness theory because the predictions would otherwise become quite hard to test. The talk will discuss what the reproductive interests of males are in terms of colony reproduction as derived from inclusive fitness theory. It will also consider why it is that males typically have little power and raise the possibility that there may be exceptions, in which males do have power to influence the reproductive characteristics of colonies. The talk will also consider whether the lack of male contribution to brood rearing in social Hymenoptera is due to the reproductive asymmetries caused by haplodiploidy, or is a carry over from their non-eusocial ancestors in which parental behaviour was exclusively maternal.

Sexual selection in social insects males

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Males of social hymenopterans (ants, bees and wasps) are notoriously understudied compared to queens and workers, and to the colonial societies that they form. Compared to the non-social insects and vertebrates, sexual selection has therefore hardly been studied in social insects as well. Here we present several concepts of how sexual selection theory can be adjusted to the idiosyncrasies of social insects and how predictions of the theory can be tested by comparative analysis or by specific experiments. Scattered data collected from the literature indicate that sexual selection is indeed operating in social Hymenoptera, in spite of males being short-lived and generally unable to monopolize groups of females. As we point out, the *Apis* honeybees are of specific interest because they have obligatory multiple mating of queens, so that sperm competition and cryptic female choice can be studied.

The males of the stingless bees: Their origin and behaviour

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The Meliponini, or stingless bees, form a diversified group of highly social bees. There are about 400 species in 50 genera. Almost all species have colonies headed by a single monandrous queen. Sociobiological theory, therefore, predicts extensive worker reproduction. However, the stingless bees are far from uniform in this character. We will discuss the occurrence and function of worker egg laying. In a limited number of genera workers do produce sons, but then there often exist also counter-strategies of the queen. Adult males soon leave the colony. Very little is known about their further life, including their mating behaviour.

Male behaviour and physiology in a polyandrous bumble bee

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Bumble bees are a valuable model system for the study of male mating behaviour in social bees. Because mating can be observed under laboratory conditions, it is possible to measure many aspects of mating that simply cannot be seen in other social bees. While most bumble bees are monandrous, at least one species, *Bombus hypnorum*, exhibits polyandry.

In this talk I will discuss variation in copulation duration – an aspect of mating that is under male control – across and within two populations of *B. hypnorum*. Like its monandrous congener, *B. terrestris*, males of *B. hypnorum* produce a mating plug that may act to inhibit remating by queens. Preliminary examination of the accessory gland, which produces the mating plug substance, suggests that physiological variation among males exists in their ability to manipulate female mating patterns. Finally, I will discuss comparative data on mating behaviour in bumble bees.

The mating systems and behaviour of European social and not-so-social bees

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In addition to its numerous honey bee (*Apis mellifera*) races, Europe holds a rich diversity of other bee species, some of which are social, many of which are solitary and a fair proportion of which are cleptoparasites of other bees. Their mating systems and male mating behaviour are, where known, equally varied.

Here I shall compare and contrast the mating system of the honey bee with that of other European bees, using personal researches on andrenid and halictid bees as well as published records. Data are provided by direct observation in the field and by inference from genetic analyses of mating structure. The conceptual framework of Alcock *et al.* (1978, *Zoological Journal of the Linnean Society* 64, 293-326) is extended to help interpret male mating behaviour. My aim is to shed light on the factors shaping variation in male mating behaviour and, in so doing, help to explain how and why the mating system of the honey bee is special.

The morphology of the male accessory glands of *Apis*

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Mating in all *Apis* species occurs during flight with queens being highly polyandrous. During copulation the male everts his endophallus successively. This endophallus consists of three major parts: the bulbus accompanied by the lobe, the cervix, the vestibulum with cornua. After full eversion, the paralysed drone becomes separated from the queen, but leaves secretions from several glands (mucus glands, cornual glands and the bulbus) in the queen, known as the mating sign. Because of the complicated mating process of different *Apis* species, we investigated the morphological organization of the endophallus and its glands in order to understand the function of the various parts. We also investigated the mucus glands. All glands change with sexual maturation of the drones. In the mucus glands, the muscle layer thickens while the gland cells atrophy. Our preliminary research indicates that the gland epithelium of the bulbus invaginates and forms a tube. This tube secretes an annular structure inside the bulbus that is probably involved in keeping secretions together for the production of the mating sign. The cornual glands are similar in all studied species and produce a sticky orange secretion containing lipids.

Effect of rearing conditions on the reproductive fitness of *Apis mellifera* drones

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In colonies of *Apis mellifera* two types of drones occur. The majority are large drones which are reared in special drone brood cells. Small drones which derived from worker brood cells are found in lower numbers. We compared the effect of good and poor larval rearing conditions and the effect of foster conditions for immature drones on the variability (within and between both drone types) of the following fitness parameters:

1. Number of spermatozoa;
2. Vitality of spermatozoa;
3. Excess power index (integrating body mass, thorax to body mass and wing surface area);
4. Duration and frequency of mating flights.

“In the right time at the right place” – behavioural adaptations of honeybee drones to an extreme male biased sex ratio

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At the drone congregation area (DCA) of *Apis mellifera*, the sex ratio is extreme: 8.000 to 15.000 drones are circling high in the air, waiting for an encounter with a virgin queen. Under these conditions, the *Apis* drone must use even very slim chances to maximize his mating success. Not to miss the first and the last virgin queen, the flight activity of drones starts earlier and ceases later than the queens' mating flight period. Timing of drones' mating flights depends rather on the individual internal clock than on the social Zeitgeber of the colony. Cross fostered drones of *Apis koschevnikovi* and *Apis cerana* maintained a species specific drone flight activity. Further, *Apis mellifera* drones were transferred from a flight room with a shifted light cycle to colonies outside. These drones maintained their the shifted flight activity unchanged for the first day. Later, they gradually adjusted to the natural activity rhythm. In a steep Alpine valley, *Apis mellifera* drones had the choice between 2 DCAs, one near and the other more distant. The drones preferred the nearer DCA. This energetic choice in relation to flight distance permits the drone to prolong his presence at the DCA and increases his chances to mate.

How to win a queen – species specific mating strategies of *Apis* drones

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In *Apis* species the sex ratio is highly male biased. Hundreds or thousands of drones fly on drone congregation areas (DCA) competing for each virgin queen. Some parameters of drone flight characteristics were collected at the colony: drone size, excess power index (integrating body mass, thorax to body mass and wing surface) and flight duration. By a stereoscopic video equipment drones of *Apis mellifera*, *A. dorsata*, *A. cerana* and *A. koschevnikovi* drones were recorded following a moving queen dummy (2.5 m/sec). Flight speed, duration of queen pursuit, behaviour during queen pursuit (size of drone groups), and behaviour of successful drones (grasping the dummy) were analysed.

Weight and excess power index seems not to correlate with flight duration and flight speed. *A. dorsata* drones (155 mg) were the fastest flyers (4.3 - 4.7 m/s) and *A. koschevnikovi* (106 mg) were the slowest (2.7 - 2.9 m/s) while for *A. cerana* (83 mg)

and *A. mellifera* (220 mg) a medium flight speed was recorded. Drones of *A. koschevnikovi* and *A. mellifera* formed large pursuing groups, *A. cerana* and *A. dorsata* drones showed preferably individual chasing behaviour. All species tended to avoid collisions, so scrambled competition did not occur. The different strategies are to be discussed considering environmental selective forces as well as intrinsic constraints like degree of polyandry.

Differences in the metabolism of worker and drone bees in *Apis mellifera* L.

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With respect to their physiology, honeybee drones have not been investigated as intensely as workers. Their quite limited function is to produce sperm and to mate with queens. In contrast to drones, workers perform an enormous variety of tasks. They clean the hive, tend the brood, forage for food, nourish the queen, the drones and the other workers, and work for nest homeostasis. The investment of workers raising individual drone larvae is higher than that for worker larvae. Adult drones ingest much less pollen, compared to workers and the proteolytic activity in their midgut runs on a low level in parallel with this reduced feeding on pollen. Nevertheless their body protein content increases with age, demonstrating the importance of proteinaceous jelly feeding by the workers' hypopharyngeal glands, which are absent in drones. These glands shift their function from brood food production in young workers, to the production of carbohydrate digesting enzymes in old workers. One of these enzymes, amylase, enables the workers to quickly degrade starch, and to utilise it even in flight metabolism, which is not the case in drones. While we have information about the passage of liquid and solid food in the workers' gastrointestinal little information is available for drones. Differences between workers and drones are found in their body's glycogen content – which is rather low in both gender – and in the content of free amino acids in the hemolymph, being significantly higher in drones than in workers.

Thermographic measurement of the body temperature of honeybee drones and workers starting and landing at the hive entrance

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Honeybees are insects with the ability of endothermic heat production. Before leaving the hive they have to heat up their thorax to be able to take off. Outside the hive their body temperature is influenced by ambient temperature (T_a) and solar

radiation. Drone honeybees are approximately twice the size and weight of workers. Therefore, we investigated, whether the body temperature of departing and arriving drones at the hive entrance is also higher than in workers.

The body temperature of starting and landing bees was measured at the entrance of a standard hive with infrared thermography (FLIR, AGA782 SW and ThermaCam SC2000). When leaving the hive as well as when arriving the drones had significantly higher thorax temperatures (means upon leaving: 39.6-43.1 °C; arriving: 37.5-40.3 °C) than the workers (leaving: 35.0-36.9 °C, arriving: 34.8-38.1 °C; *t*-test, all $p < 0.0001$; $T_a \sim 20-26$ °C). Comparing the temperature of starting and landing bees, drones with only one exception (0.1 °C) were always warmer in the thorax at starting (0.9-2.1 °C). In worker bees the results were not so uniform, the thorax temperature was the same or higher when starting (2.1 °C) or it was smaller (1.2-1.8 °C, all $p < 0.0001$).

The results show that the heavier drones (ca. 120-300 mg) are warmer than worker bees (ca. 80-165 mg) when departing and returning to the hive. Therefore, we suppose that drones are warmer than workers also during flight.