

THE CALMING NATURE OF REPRODUCTORY DOMINANCE OF THE QUEEN IN THE HONEYBEE COLONY (*Apis mellifera* L.)

Z b i g n i e w L i p i ń s k i

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S u m m a r y

The observation that withdrawal of the queen from the colony of western honeybees (*A. mellifera* L.) cause it unusual agitation connected with subsequent ovary activation and unfertilized egg laying by sterile workers (Winston 1987) indicates that the calming effect of queen substance (understood as a full blend of its pheromones) enforced by a similarly acting blend of open brood pheromones known as “pheromonal queen control”, is the main device of reproductive dominance of the queen. Consider that emotional system of the honeybee governs and orchestrates it behaviour with physiology.

Based on this hypothesis the author presents possible signaling pathways of this reproductive dominance in context of so called Lee-Booth effect. Last findings indicate that worker bee tissues contain some “higher” animal reproductive (FSH, LH) and sex hormones (testosterone, E₂). In view of above hypothesis the author concludes that role of evolutionary conserved gonadotropic and sex hormones in regulation of reproduction in honeybees should be the object of more intensive studies.

Keywords: honey bee, honeybee queen, reproduction, FSH, LH, GnRH, E₂, Lee-Booth effect.

INTRODUCTION

The workers of eusocial Hymenoptera are normally sterile, but under certain conditions this is not true (Bourke 1988). For instance the honeybee workers *Apis mellifera* L. usually do not reproduce, but can activate their ovaries under queenless conditions to produce male offspring (Winston 1987). As an exception to the rule, laying workers of the Cape honeybee, *A. m. capensis* Esch., can parthenogenetically produce diploid female offspring (Neumann and Moritz 2002).

The observation that withdrawal of the queen from the colony of western honeybees (*A. mellifera* L.) cause it unusual agitation (reviewed by Lipinski 2006 a, 2001) connected with ovary activation and unfertilized egg laying by sterile workers (Winston 1987) indicates, that repro-

ductive dominance of the queen in honeybee colony is rooted in suppression of neuronal circuits of the emotional system (NCES) of worker bees by her calming pheromones (Lipiński 2006 a, b). Consider that emotional system of the honeybee can govern and orchestrate it behaviour with physiology. The significant behavioural symptoms of this phenomenon is emotional piping of queenless laying workers of *A. m. ligustica* (Ohtani and Kamada 1980) as result of motoric abreaction of surplus of emotional agitation.

PHEROMONES OF THE QUEEN AND YOUNG BROOD IN SIGNALLING PATHWAYS OF SUPPRESSION OF WORKER REPRODUCTION

Consider that: (1) – queen substance (QS) – understood as a full blend of her calming pheromones is able to suppress

NCES of worker bees (Lipiński 2006 b), (2) NCES govern stereotypical expression of innate behaviours (instincts) (Lipiński 2006 a) (3) – NCES orchestrate these behaviours with physiology (reviewed by Lipiński 2006 a), an assumption arise that QS can suppress both, reproductive behaviours of workers (e.g. queen cell building, queen rearing etc.) and physiology of ovary activation and egg laying as well.

However observations that application of synthetic mandibular pheromone (sQMP) can be accompanied by suppressing queen cell-building behaviour in the field (Grozinger et al. 2003) and by ovary development in caged bees (Shelley et al. 2003) indicate that in some cases this suppression is not strong enough. Mostly due to excessive emotional agitation of bees which makes them more resistant to this calming effect (Lipiński 2001). This explanation confirms fact that sQMP do not inhibit queen rearing in terms of advanced swarming stress (reviewed by Lipiński 2001) and do not suppress ovary development in (highly agitated) queenless colonies of *A. mellifera* L., (Willis et al. 1990).

The psychobiological nature of the discussed calming suppression of workers reproduction confirms also, that: not only a natural blend of queen pheromones (QS) – especially extract of queen mandibular glands (nQMP) (Winston 1987) but also similarly acting pheromones of open brood (BP) can suppress, ovary activation in sensitive workers (reviewed by Lipiński 2006 b) and elevate their response thresholds (Pankiv et al. 1998). Significantly for this calming phenomenon, both QS (Kaatz et al. 1992, Pankiv et al. 1998) and BP (Le Conte et al. 2000) can suppress juvenile hormone (JH-3) and slow down their behavioural development. This is because JH-3, as mediator of emotional responses of honeybees can influence per-

ceptive abilities of workers (reviewed by Lipiński 2006 a). Especially in stress conditions (Lin et al. 2004). For instance its high level enhance perceptive abilities of swarming stress (Zeng et al. 2005, Lipiński 2001).

It seems that as a result of that calming/emotional reason, in queenless colonies of less stress sensitive European workers ovary development did not begin until most or all the brood from the previous queen had emerged (consider calming effect of BP), but ovaries developed in extremely stress sensitive Africanized workers (more resistant to this calming effect) while uncapped brood was present and colony was in the process of queen replacement (De Grandi-Hoffman and Schneider 2002).

What is more, observations that (1) - laying queens (Fahrbach and Robinson 1996) and laying workers (Robinson et al. 1992) in queenless colonies have a low level of JH-3 titers in their haemolymph, (2) - JH-3 do not increase ovary development in queenless and broodless colonies (Robinson et al. 1992), (3) – JH-3 analogue (pyriproxyfen) inhibits vitellogenin synthesis (Lucimara et al. 2000), (4) - JH-3 do not make ovary activation and egg laying (Mohameddi et al. 1998, Winston and Slessor 1998) strongly suggest that there is no evidence that JH-3 acts as a traditional gonadotropin (Robinson and Vargo 1997) and that in honeybee JH-3 has partly lost in evolution its gonadotropic effect if it ever was.

However the initiating role of some JH titers in ovary development as result of some kind of emotional arousal of the aforementioned NCES can not be excluded, because low JH-3 titers in workers permit the onset and accumulation of vitellogenin (Pinto et al. 2000). The more so that, reproductively dominant individuals of *A. m. capensis*, which are resistant to queen control (Lipiński 2006 b), fre-

quently produce this substance which seems to precede ovary activation (reviewed by Wossler 2002).

Presented here the hypothesis of calming mechanism of social (behavioural + reproductive) dominance of the queen over workers remains linked with the observation that emotional piping of workers after queen loss (Ohtani and Kamada 1980), is connected with increase of dopamine (Sasaki and Nagao 2001) and tyramine (Sasaki and Nagao 2002) in brain levels. What is more dietary dopamine causes ovary activation in queenless *Apis mellifera* workers (Dombrowski et al. 2003) despite the low JH titers and rates of biosynthesis (Robinson et al. 1992). It is noteworthy that correlation between brain dopamine and the ovarian development in queenless workers was previously suggested by Harris and Woodring (1996, 1995).

Interestingly it is as result of that of excessive emotional arousal of queenless workers (Lipiński 2006 a) that some unusual behaviours appear. For instance: (1) - irregular egg laying, (2) - emergency queen cells construction with dead drone larvae (3) - small cups built over pollen or (4) - an egg is laid on the pollen mass (Morse and Hooper 1985).

The psychobiological nature of the mechanism of calming suppression of workers reproduction discussed above confirms also fact that signals arise from the tergal glands of queens can also inhibit worker reproduction (Wossler and Crewe 1999).

THE POSSIBLE ROLE OF GLIKOPROTEINE HORMONES IN REGULATION OF HONEYBEE REPRODUCTION

Research on the hormonal regulation of various vital processes in invertebrates started relatively late (Cymborowski 1992). In insects, the molecular mechanisms behind reproduction are, so far, only

poorly understood (Grimmelikhuijzen et al. 2000). Control of gonad development in insects requires juvenile hormone, ecdysteroids and a peptidic brain gonadotropins (De Loof et al. 2001). What is more, the same hormones regulate growth and metamorphosis and control reproduction during adult life (reviewed by Cymborowski 1992).

Compared to vertebrates the situation in insects with respect to the molecular structure of gonadotropins is far less uniform. Follicle Stimulating Hormone (FSH) and Luteinizing Hormone (LH) of vertebrates are glycoproteins that are synthesized and released from the anterior pituitary (Grimmelikhuijzen et al. 2000). They stimulate gonad development, the production of progesterone or of sex steroids (De Loof et al. 2001).

Significantly, neurosecretion from pars intercerebralis of the insect brain regulates certain stages of the reproductive process due to its gonadotropic properties (reviewed by Cymborowski 1992). What is more in *Drosophila melanogaster*, two G-protein coupled receptors, structurally related to the mammalian glycoprotein hormone receptors, have been identified (De Loof et al. 2001).

Consider that (1) - "invertebrate and vertebrate nervous systems appear to utilize similar intercellular signal molecules" (Stefano 2002), (2) - glycoproteine gonadotropic hormones such as FSH and LH were found in honeybees (Zhou and Wen 2002), (3) - measurable immunore-activities characteristic for sex hormones such as testosterone (T) and estradiol-17 beta (E₂) were found by Zhou and Wen (2002), (4) - testosterone was found in royal jelly (Vitteck and Slomiany 1982), 5 - E₂ is also produced by silkworm (Keshan and Ray 2001), (6) - E₂ can encourage egg production in mature female of *Bombyx mori* (Ohnishi et al. 1985), an assumption arises that "unsolved problem of hormonal

regulation of reproduction in insect” (Hauser et al 2000, Grimmelikhuijzen et al. 2000, Robinson and Vargo 1997) can be solved base on hypothesis that this regulation can work with most evolutionary conserved molecules, such as: FSH, LH, E₂, testosterone or even gonadotropin releasing-hormone (GnRH) which is an unique neuropeptide conserved through 500 milion years of evolution (Chen et al. 2002) and duplicated twice prior to the emergence of teleost and most probably tetrapods (Okubo and Aida 2001). Significantly honeybees (Hymenoptera) diverged from Diptera and Lepidoptera 300 million years ago, whereas last common ancestor with humans was 600 milion years ago (Grimaldi and Engel 2005).

It is worth mentioning that GnRH producing neurons, directly sensitive to changes in social context (Robinson 1999) link the brain to the reproductive system (Dubois et al. 2002) through the control of release of LH and FSH. These last two hormones directly regulate ovary activity (egg laying) and sex hormone production (e.g. E₂) with accompanying changes in behaviour.

Thus through the calming suppression of workers GnRH producing neurons (or other similar releasing hormone) by QP and BP, the honeybee queen halts workers FSH and LH producing neurons and egg laying as well. Especially because: (1) - by using monoclonal antibodies directed against different epitopes of human LH, Verhaert and De Loof (1986, 1988) observed immunopositive reaction in the brain as well in the CC of the *Periplaneta americana*, (3) De Loof et al. (2001) observed also stimulating effect of insect brain extract on testosterone production by mouse Leyding cells (4) – LH and FSH – immunoreactivity was also discovered in brains of *Locusta migratoria* and

Neobellieria bullata (Thuenis et al. 1989), (5) - levels of LH, and E₂ in worker bees emerged and developed in the absence of the queen, rose at the third day (Zhou and Wen 2002), (5) – the content of FSH of nursing bees from the day of emergence is more or less the same with a decreasing trend, while it is significantly higher in forager bees (Zhou and Wen 2002).

The presence of GnRH neurons in bee brain seems to confirm discovery of Hauser et al. (2000) who cloned from *Drosophila melanogaster* receptor that is structurally and evolutionary related to the mammalian GnRH receptor. They also found that the fruit fly produces at least two receptors that are structurally and evolutionarily related to the LH and FSH. It means DLGR-1 (*Drosophila* Leu-rich repeats containing G protein-coupled receptor-1 which transduce extracellular signals into cellular physiological responses) and DLGR-2. However it is not clear whether these receptors are involved in the control of insect reproduction (De Loof et al. 2001).

It seems also possible that calming effect of QP + BP can suppress NCES connected with GnRH producing neurons via inhibition of synthesis of excitatory aminoacid glutamate. Especially because glutamate (reviwd by Harris and Woodring 1992, Bicker et al. 1988) binds to NMDA (N-methyl-D-aspartate) receptors resulting in the influx of Ca²⁺, thereby increasing nitric oxide synthase (NOS) activity, in a situation when nitric oxide may play a role in GnRH regulation (Dhandapani and Brann 2000, Nelson et al. 1997). Consider that glutamate is believed to elicit sexual behaviour (Dhandapani and Brann 2000), whereas NO can freely diffuse through cellular membranes (Cole et al. 2002).

**THE POSSIBLE ROLE OF THE
LEE-BOOT EFFECT-LIKE
MECHANISMS IN REPRODUCTORY
DOMINANCE OF THE HONEYBEE
QUEEN**

Studies on mammals have revealed that the regulation of reproductive development often involves chemical signals that either advance or delay maturation (Stern and Mc Clintock 1998). For instance androgen-dependent chemical activators accelerate the onset of puberty, while adrenal gland-dependent inhibitors delay it. These signals are thought to be perceived by the vomeronasal organ, which sends projections to the accessory olfactory bulb. Information is then transmitted than to higher brain centres that ultimately control the release of ovarian luteinizing hormone. This way for e.g. primary pheromones of mice perceived by others via the vomeronasal organ are able to activate their brain centres cause releasing luteinizing hormone (LH) what is enables fit time of their reproduction to changes in density and sexual composition of the group (Lomas and Keverne 1982, Darney et. al 1992). The phenomenon known as Lee-Boot effect (Turner and Bagnanara 1978).

In the above context the assumption that reproductive dominance of single molerat female over her subdominants does not result from their reduced pituitary secretion of LH or decreased sensitivity to hypothalamic GnRH (Bennett et al. 1997) seems to suggest that reproductory dominance of the honeybee queen over workers, which reminds molerat "queen" dominance, can have a more complicated and socially supported psychophysiological context. However, the assumption that some kind of Lee-Booth effect can control worker bee and subdominant molerat female reproduction can not be excluded.

CONCLUSIONS

Judging from all above presented studies and deliberations I venture to put forward the hypothesis that the calming effect of QS, understood as a full blend of its pheromones enforced by a similarly acting blend of BP pheromones (reviewed by Lipiński 2006 a, b) known as "pheromonal queen control" (Keller and Nonack 1993), can manage reproductive and behavioural dominance of the queen in the honeybee colony.

In view of this assumption proposed role of evolutionary conserved gonadotropic and sex hormones in regulation of reproduction in honeybees should be the object of more intensive studies.

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USPOKAJAJĄCA NATURA REPRODUKCYJNEJ DOMINACJI MATKI W RODZINIE PSZCZELEJ (*Apis mellifera* L.)

Z b i g n i e w L i p i ń s k i

S t r e s z c z e n i e

Dobrze znany fakt, że usunięcie matki z rodziny pszczelej powoduje nadzwyczajne pobudzenie nerwowe robotnic wraz z późniejszym składaniem przez nie niezapłodnionych jaj (Winston 1987) wskazuje, że uspokajający wpływ feromonów matki, wspomagany przez podobnie działające feromony młodego czerwiu, znany jako „feromonalna kontrola ze strony matki” (ang. pheromonal queen control), stanowi główny mechanizm reprodukcyjnej dominacji matki w rodzinie pszczelej. Mając jednocześnie na uwadze, że system emocjonalny pszczoły miodnej steruje jej zachowaniami, zgrywając je z odpowiednimi reakcjami fizjologicznymi.

Bazując na tej hipotezie, autor przedstawia możliwe drogi jakimi substancje sygnałne sterują tą dominacją w kontekście efektu Lee-Booth’a. Potwierdzeniem tej hipotezy wydają się być ostatnie odkrycia wskazujące, że tkanki pszczoły miodnej zawierają typowe dla tzw. „zwierząt wyższych” hormony gonadotropowe (FSH, LH) oraz płciowe (estradiol - E₂ testosteron).

W świetle powyższej hipotezy autor wnioskuje, że rola ewolucyjnie starych hormonów gonadotropowych i płciowych w regulacji rozmnażania się pszczół winna stać się obiektem wzmocnionych badań

Słowa kluczowe: pszczoła miodna, matka pszczela, FSH, LH, GnRH, E₂, Efekt Lee-Booth’a.