



Reproductive regulation in an orchid bee: social context, fertility and chemical signalling



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ARTICLE INFO

Article history:

Received 10 January 2015
Initial acceptance 5 February 2015
Final acceptance 13 April 2015
Published online xxx
MS. number: A15-00021R

Keywords:

chemical signalling
dominance behaviour
Euglossa melanotricha
social evolution
status reproductive

In social insects, the communication of social status helps individuals evaluate each other's reproductive potential, thus reducing conflict. Queens communicate their status through chemical signals, and the responses of workers to these signals include the suppression of ovarian activation. In most species of primitively social insects, dominant individuals indicate their status through aggressive behaviour, which also inhibits reproduction in workers. In some species, which lack queen–worker dimorphism, chemical signalling may act synergistically with agonistic interactions to establish the division of labour between females. Here, we investigated which mechanisms are involved in reproductive regulation in the orchid bee *Euglossa melanotricha*. Our long-term observations showed that dominant females monopolized egg laying and were able to recognize the eggs of subordinates. The overt aggression towards subordinates affected the egg-laying behaviour of these females but did not inhibit their ovarian development. We found that dominants maintained their monopoly on reproduction even after their experimental removal. When subordinates were removed, the productivity of the nest was reduced significantly, indicating clear benefits of the division of labour between females. We then analysed the chemical cuticular profile of the females and found that variation in the composition of hydrocarbons reflected the social status of the different individuals. The results of this study suggest that chemical signals evolved as honest signals and that workers restrain themselves from reproducing. This reduces reproductive options but increases selection pressures on the workers to obtain indirect fitness.

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The evolution of fertility signals in social species with reproductive division of labour provides a mechanism for group members to evaluate an individual's reproductive status (Smith, Hölldobler, & Liebig, 2009). In social insects, for example, the process by which the presence of a productive breeder affects the behaviour of other group members has been previously described (Liebig, 2010; Nunes et al., 2014). These studies have demonstrated that honest signalling among competing individuals can increase colony fitness. However, conflicts are known to be more likely when rivals are reproductively equivalent (Ratnieks, Foster, & Wenseleers, 2006). Conflict can be expressed through physical dominance, which is a fundamental aspect of the establishment of the division of labour between breeders and nonbreeders (Liebig, Peeters, & Hölldobler, 1999). On the other hand, overt dominance

is potentially deleterious because individuals involved in agonistic interactions may be less productive than noncompeting ones (Gobin & Ito, 2003; Zanette et al., 2012).

In social insects, cuticular hydrocarbons constitute the main source of the signals used for communication and chemical recognition (Blomquist & Bagnères, 2010). The occurrence of specific chemical compounds on the cuticle, which can be used for communication of the activation of the ovaries or social status have been reported in several studies (Nunes et al., 2014; Teseo, Kronauer, Jaisson, & Châline, 2013). Reproductive signalling is particularly important when a group of totipotent fertile females dispute dominance (Zanette & Field, 2009). Empirical evidence indicates that the unidirectional nature of the dominance hierarchy in primitively eusocial hymenopterans evolved via coercion and secondarily through odour recognition (e.g. *Polistes*: Downing & Jeanne, 1985; *Ropalidia*: Premnath, Sinha, & Gadagkar, 1996; *Dinoponera*: Monnin & Peeters, 1999; *Bombus*: Amsalem & Hefetz, 2010).

According to the honest signal hypothesis, the odours emitted by reproductive females advertise both mating status and fertility (Keller & Nonacs, 1993), and the response of the other members of

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the group may be proportional to the reproductive status of the queen (Evison, Ferreira, d'Etorre, Fresneau, & Poteaux, 2012). The ethophysiological effects of putative queen pheromones have been demonstrated in workers of some species of ants, bees and wasps (Holman, Jørgensen, Nielsen, & d'Etorre, 2010; Nunes et al., 2014; van Oystaeyen et al., 2014; van Zweden, Bonckaert, Wenseleers, & d'Etorre, 2014). Recent evidence also indicates that the cuticular hydrocarbons of the queen pheromone are conserved over a range of eusocial taxa, suggesting that the fertility-associated signal is an ancestral trait, and was probably present in the ancestral solitary insects that gave rise to the social insects (van Oystaeyen et al., 2014).

The orchid bees (tribe Euglossini) are considered a key group for understanding the evolution of eusociality in the corbiculates (Apini + Meliponini + Bombini), because they range from solitary to communal to primitively eusocial species (Augusto & Garófalo, 2010; Cardinal & Danforth, 2011; Cocom Pech, de J. May-Itzá, Medina Medina, & Quezada-Euán, 2008; Soucy, Giray, & Roubik, 2003). Previous studies have speculated that solitary behaviour in the orchid bees would be an evolutionary reversion, with some *Euglossa* species retaining some eusocial traits (Cardinal & Danforth, 2011). Other reports, however, suggest that eusociality was inherited from a eusocial ancestor to all corbiculates (Canevazzi & Noll, 2014; Chavarría & Carpenter, 1994; Noll, 2002; Zucchi, Sakagami, & Camargo, 1969). Therefore, the study of behavioural biology of orchid bees can illuminate the interpretations of the evolution of eusociality in corbiculate bees.

Despite the existence of an extensive database for bumblebees (Ayasse et al., 1999), honeybees (Wossler & Crewe, 1999) and stingless bees (Nunes et al., 2014), no evidence is available on the possible chemical modulation of social relationships in bees of the genus *Euglossa*. In this study, we investigated which factors contribute to the social structure of the nest of an orchid bee, *Euglossa melanotricha*. We tested how reproductive dominance is established and maintained in these simple societies. We predicted that, as in other primitively eusocial species, overt aggression towards subordinate individuals would affect egg-laying behaviour of these females but would not inhibit their ovarian development. In addition, we verified whether the dominance status of individuals was reflected in their cuticular chemical profile using a series of removal experiments.

METHODS

Life History

Euglossa melanotricha is a medium-sized bee (body length 13 mm) commonly found in open areas of savannah habitat in Brazil and Bolivia (Nemésio, 2009). Solitary females found new nests, or females can reuse an old nest, resulting in multifemale nests. Reused nests are occupied by two to five females. All females can potentially mate and lay eggs, although only one female becomes the main reproductive dominant (Andrade-Silva & Nascimento, 2012). A process of nest reuse is initiated when two newly emerged females remain in their natal nest and one begins to reproduce. In the present study, the mean \pm SD duration of the reuse process (from the time a female started foraging for resin to her final oviposition) was 46.4 ± 14.9 days (range 18–79 days, $N = 30$ nests). Following reuse, the females remained in the nest without engaging in any further outside activities. This period of inactivity lasted from 15 to 63 days (mean \pm SD = 34.11 ± 11.7 days). To control for the number of females in each reused nest, we removed the females during this period of inactivity, and waited for the next nest reuse after emergence of new females.

Nests, Bees and Observation Procedures

Fourteen multifemale nests of *E. melanotricha* were housed in wooden boxes ($12 \times 10 \times 8$ cm) covered with a glass lid. Each box had a circular opening of 1 cm in diameter that allowed the bees to fly freely, following the same transfer protocol as that adopted by Andrade-Silva and Nascimento (2012).

The nests were observed prior to the experiments in order to identify the roles of the different occupants. For each nest, observation sessions followed two methods: (1) all-events records, in which we recorded every performance of a selected set of behaviours by every individual, and (2) focal individual observations to record the behavioural state of each individual. Both methods followed the same schedule: three times a week during January 2013 and April 2013.

We registered behaviour continuously through a combination of digital video footage captured using mini-cameras (Citrox 5001 colour digital day/night). The cameras were positioned on top of the glass lid, approximately 15 cm above the cells. We marked all bees on each nest with unique spots of quick-drying nontoxic coloured paint (Magic[®]) on their thorax for individual identification.

During the course of study, we observed 12 nest invasions by foreign females. So, the distinct groups of females (resident dominant versus subordinates, dominant invaders versus subordinate) were analysed separately.

We used the data for the focal individuals to compute the proportion of time spent by each bee in a number of common behaviours, and data from all-events sessions to calculate the hourly rates of the less common behaviours. We focused on the following four behaviours described (see Table 1). (1) Dominance: 10 pairs of females with a stable reproductive structure (i.e. one individual had been dominant for several weeks) were videotaped for 24 h continuously (240 days; 5760 h; 12:12 h light:dark cycle). We focused on the performance of the dominant female, including behaviours as attacking, heading, overflying, pursuing and cannibalism of the subordinate's eggs. We computed the rates of dominant acts for each bee, after correcting for the proportion of time bees spent at their nests, on a given day. Results were analysed using Wilcoxon exact tests. (2) Nondominance or nonaggressive behaviour: active components of nondominant interactions of the pair; that is, antennating and approaching. We computed rates of nondominant interactions for each bee relative to their dominance behaviours. (3) Subordinate behaviour. (4) Other activities: proportion of time that a bee engaged in activities such as foraging trips or remained inside the nest engaging in activities such as resting and cell provisioning for egg laying.

Ethical Note

We used 108 females in this study (30 dominants, 30 subordinates, 12 invaders and 36 additional females that were used in removal experiments; see below). Research was carried out under permission of IBAMA (license number 19575).

Removal Experiment 1: Dominant Individuals

We conducted the experimental sessions in five repetitions for each time interval ($N = 10$ nests; see Supplementary Table S1) between May 2013 and October 2013. Each repetition focused on a new process of nest reuse, following the emergence of two new females. We manipulated the number of females, so that only two females were monitored in each experiment. In this case, we removed any additional females (one to three females per trial) that emerged from the nest after we identified the resident pair of individuals.

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