

Order of adult eclosion is a major determinant of reproductive dominance in the allodapine bee *Exoneura bicolor*

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(Received 27 April 1992; initial acceptance 13 July 1992;
final acceptance 22 January 1993; MS. number: 4101)

Abstract. Overwintering colonies of the allodapine bee *Exoneura bicolor* are characterized by marked reproductive differentiation among female nestmates. Previous work has shown that reproductively dominant females are nearly always the first females to reach adult eclosion (i.e. to hatch from the pupal case) among their brood cohort. This study examines whether this relationship is causal, or whether it reflects a correlation between eclosion order and other unknown factors that may be the actual determinants of dominance. Female pupae were transferred from natural to artificial observation nests prior to adult eclosion. Eclosion order among these females was investigated in experimental colonies which were subjected to one of four treatments. In one treatment pupae were allowed to eclose without experimental manipulation. In two treatments the development of older pupae was delayed by selective refrigeration, and in the last treatment older pupae were removed entirely. There were no effects of treatment type and no interaction between treatment type and eclosion order. In all treatments, first eclosed females became reproductively dominant.

Considerable work has been carried out on caste determination in eusocial apid and halictine bees (see reviews by Engels & Imperatriz-Fonseca 1990; Hartfelder 1990; Michener 1990a; Röseler & Van Honk 1990), although comparatively little is known about caste determination in one of the most socially diverse groups, the tribe Allodapini (family Anthophoridae). The allodapines are unique among bees in that larvae are reared progressively in a single communal chamber, leading to a high degree of contact between all adult and immature nest occupants (Michener 1990b). In the sister tribes, Xylocopini and Ceratinini, social colonies frequently consist, at least initially, of two or more reproductively active females, and reproductive division of labour may be preceded by agonistic interactions and reciprocal egg eating (see review by Michener 1990b), and to this extent reproductive differentiation appears to be largely mediated by behavioural interactions.

The Australian allodapine genus *Exoneura* contains at least several species which have high levels

of cooperative nest use and cofounding (Michener 1965; Houston 1977; Schwarz 1986, 1988). In *E. bicolor*, reproductive differentiation in older colonies (second or later year of nest usage) is marked. Such differentiation initially involves the appearance of 'winter egg-layers', i.e. one to a few inseminated females in each colony which undergo comparatively accelerated ovarian development during winter and pheromonally inhibit ovarian development of their nestmates (Schwarz et al. 1987a; O'Keefe & Schwarz 1990). This differentiation does not seem to be accompanied by agonistic interactions. Schwarz & O'Keefe (1991) investigated the role of age in reproductive differentiation in *E. bicolor* by monitoring uncaged colonies in a semi-natural environment. In nine out of 10 colonies the reproductively dominant female was the first or equal-first female to reach adult eclosion (i.e. to hatch from the pupal case) among her natal cohort. Because most broods eclose over a period of less than 2 weeks but egg laying does not commence until some 5–6 months later, differences in the relative adult ages of nestmates are small at the time of reproduction. Body size was weakly associated with reproductive dominance, dominant females tending to be larger. However, earlier eclosing females tend to be larger than later eclosing females (Schwarz 1987a). Using partial correlation

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