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Short communication

The biology of *Brevineura froggatti* and phylogenetic conservatism in Australian allodapine bees (Apidae, Allodapini)

S. M. Tierney, A. L. Cronin, N. Loussert and M. P. Schwarz

School of Biological Sciences, Flinders University of South Australia, GPO Box 2100, Adelaide, S.A. 5001, e-mail: Michael.Schwarz@flinders.edu.au

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Summary. We present the first data on the social biology of the allodapine bee, *Brevineura froggatti*. Colony sizes are small, and only 12.5% of nests contained more than two females. Brood rearing occurs throughout the year, including winter, as it does in the other species of *Brevineura* studied to date. In both *Brevineura* species, per capita brood production is much higher in multi-female nests than single-female nests, raising the question of why more colonies aren't multi-female. The occurrence of small colony sizes, despite large benefits to group living, differs strongly from species of the sister clade *Exoneura*. These findings, combined with previous allodapine studies, indicate conservatism in voltinism, brood phenology and colony size within, but not between, Australian allodapine genera.

Key words: Allodapini, *Brevineura*, *Exoneura*, social evolution, phylogenetic conservatism.

Comparative approaches to studying early steps in social evolution are often most informative when focussed on taxa where sociality varies within and between species and genera. The bee tribe Allodapini contains a diverse array of social forms and provides an ideal opportunity for such studies, and detailed life cycles are presently known for multiple species in the exoneurine genera *Exoneura* and *Exoneurella* (review in Schwarz et al., 1998). However, life cycle and social traits have been characterised for only one species in the remaining non-parasitic genus, *Brevineura* (Tierney et al., 1997). Phylogenetic studies (Michener, 1977; Reyes, 1998) suggest that *Brevineura* form a sister clade to *Exoneura*, with *Exoneurella* being basal. Knowledge of sociality in *Brevineura* is thus important for inferring social evolution in the Australian allodapines.

Tierney et al. (1997) showed that *Brevineura xanthoclypeata* is characterised by very small colony sizes and solitary nest founding. Egg production occurs year round and brood rearing is protracted, including larval development over winter, which contrasts strongly with species in *Exoneura* and *Exoneurella*, which are univoltine and bivoltine respectively.

In this paper we outline some aspects of the life cycle and sociality of a second *Brevineura* species, *B. froggatti* (South Australian Museum holds voucher specimens). Although our samples are small, they provide useful material for comparison with other allodapines. The difficulty in sampling this species makes it unlikely that more detailed data from this species will become available for many years.

Nests of *B. froggatti* were sampled from Cobboboonee State Forest and Lower Glenelg National Park, Victoria (38°77′S; 141°35′E). In this habitat *B. froggatti* nests in dead canes of the saw-sedge *Gahnia sieberana* and dead flower scapes of the grass tree *Xanthorrhoea minor*. Nests were collected at dawn, dusk or during rain on seven dates in 1994 (16 and 30 March, 20 April, 11 May, 11 June, 21 July and 24 August) and five dates in 1996/97 (7 October, 7 November, 4 December, 7 January and 10 February).

The mean number of adult females per nest (per sample) varied from 1.1 to 2, modal colony size was one and the maximum was five. Of the 192 nests sampled during the study, 56% contained single females and only 12.5% contained more than two females. Brood phenology is summarised in Figure 1. Egg production showed peaks in autumn and spring, but eggs were present throughout the year except for mid summer. Larvae were present throughout the year, except for late March, and pupation occurred throughout summer and autumn. Consequently, brood development is very protracted and eggs produced in early autumn do not reach adulthood until early summer, some nine or ten months later. This pattern of brood phenology is very similar to *B. xanthoclypeata*, but contrasts with all other allodapines studied in temperate areas of Australia, where egg production occurs from winter to early summer, and where larval eclosion does not usually commence until spring.

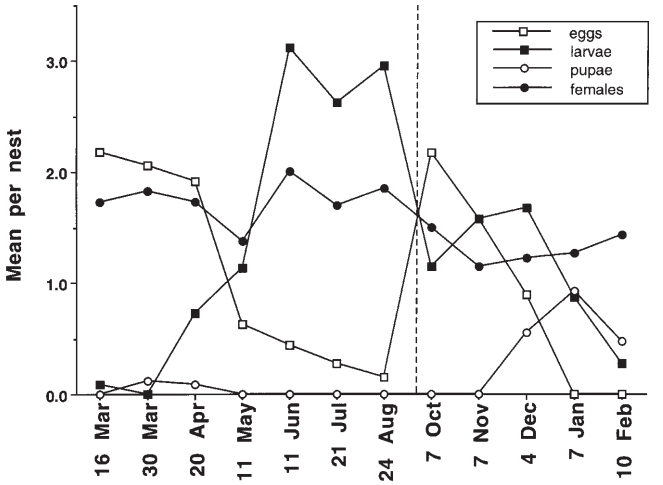

Figure 1. Mean number of immature stages per nest during the life cycle of *B. froggatti*. Data are taken from two separate collection periods, 1994 and 1996/97, separated by a dashed line

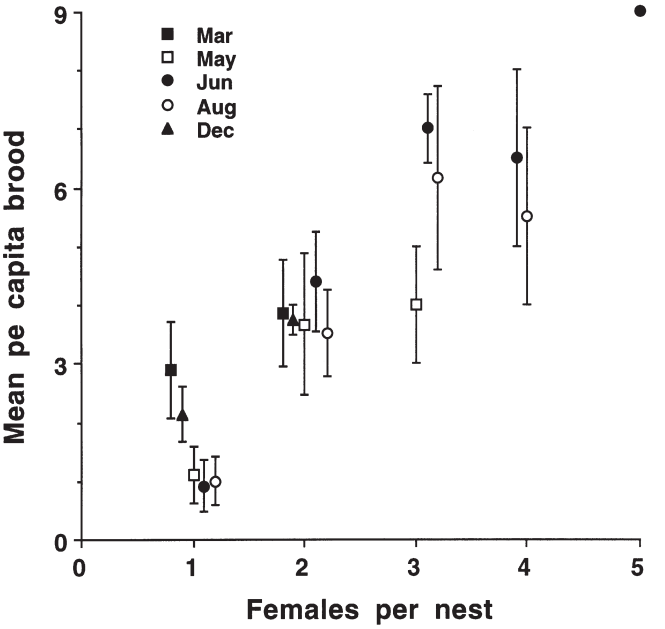

Figure 2. Mean per capita brood production (± 1 s.e.) as a function of colony size, for five samples spanning the range of seasons. Samples not graphed showed the same patterns as graphed samples

In all species of *Exoneura* that have been studied, multi-female nests show increased *per capita* production of brood compared to single-female nests, and this may explain the prevalence of multi-female nests in this genus (Schwarz et al., 1998*). Per capita* brood production (PCBP) in *B. froggatti* was calculated as the total number of brood (including callow females) divided by the number of adult females per colony. We analysed the relationship between PCBP and colony size using ANCOVA, with month as a factor (the two March samples were pooled) and the number of adult females as a covariate. Because of the rarity of colonies with > 3 females, analyses were restricted to nests containing 1 – 3 females. Results indicated no interaction between the factor and covariate ($F_{8, 144} = 0.52$, $p = 0.840$), no effect of month ($F_{8, 144} = 0.53$, $p = 0.833$), but a significant covariate effect ($F_{1, 144} = 5.42$, $p = 0.021$). The relationship between PCBP and colony size is indicated in Figure 2, which graphs data from five representative samples spread over the year. These results indicate that social nesting entails very large benefits in terms of enhanced per capita output. 2-female and 3-female colonies respectively show approximately double and triple the level of PCBP as single female colonies. It is therefore surprising that most colonies contain only one female. The same finding of small colony sizes despite large benefits of group living were found for *B. xanthoclypeata* (Tierney et al., 1997).

A recent review of Australian allodapines (Schwarz et al., 1998) suggested a high level of phylogenetic conservatism in voltinism and brood phenology within, but not among, genera. These patterns cannot be explained by habitat or climate differences associated with latitude (Schwarz et al., 1998; Cronin and Schwarz, 1999). Our data on *B. froggatti* indicates a life cycle that appears indistinguishable from *B. xanthoclypeata*. Yet, both *Brevineura* species are sympatric with, and nest in the same substrates as, *Exoneura nigrescens* and *E. robusta*, which show much larger mean colony sizes, kin cofounding, and synchronous and highly seasonal brood development (Silberbauer and Schwarz, 1995; Cronin and Schwarz, 1999). These latter species share the same life cycle and colony size patterns as other *Exoneura* species (Schwarz et al., 1998). Consequently, colony size, voltinism and brood phenology show little variation within Australian allodapine genera, but substantial variation between genera. This covariance in all three life-cycle components suggests that evolutionary changes in one may be constrained by selection on the the others. Future work needs to ask why colony sizes in *Brevineura* don't reflect the apparently very large benefits in per capita brood production arising in multifemale colonies.

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