# Latitudinal variation in the life cycle of allodapine bees (Hymenoptera; Apidae)

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**Abstract**: The life cycles of *Exoneura robusta* and *Exoneura angophorae* are examined in four populations along the eastern seaboard of Australia, where climate ranged from temperate in the south to subtropical in the north over a latitudinal range of approximately 10°. These species were univoltine throughout the range examined and most colonies produced a single brood. Timing and duration of brood development in *E. robusta* varied between sites, with brood development being more rapid in northern populations; there was only weak evidence of any effect of latitude in *E. angophorae*. All populations of *E. angophorae* exhibited a small proportion of doubly brooded colonies, but doubly brooded colonies were found only in northernmost populations of *E. robusta*. Two-brooded colonies can give rise to opportunities for sib rearing, which can alter the indirect fitness benefits for alloparental care. Our results indicate that there is an effect of climate on sociality in *E. robusta* but no, or very little, such effect in *E. angophorae*.

**Résumé** : Nous avons étudié les caractéristiques démographiques de quatre populations d'*Exoneura robusta* et *Exoneura angophorae* le long de la côte est d'Australie où le climat est tempéré dans le sud et sub-tropical dans le nord, variant d'environ 10 degrés le long d'une échelle latitudinale. Ces espèces sont univoltines dans toute la zone étudiée et la plupart des colonies produisent une seule portée par année. Le moment et la durée du développement larvaire chez *E. robusta* varient d'un site à l'autre et le développement est plus rapide chez les populations du nord; chez *E. angophorae*, cependant, la latitude ne semble avoir que peu d'effet. Chez toutes les populations d'*E. angophorae*, on a observé une faible proportion de colonies à deux portées, mais les colonies d'*E. robusta* à deux portées n'ont été rencontrées que chez les populations les plus nordiques. Les colonies à deux portées peuvent donner lieu à l'élevage d'individus sœurs, ce qui peut modifier le fitness, un bénéfice indirect relié aux soins alloparentaux. Nos résultats indiquent que le climat influence la socialité chez *E. robusta* mais ne mettent pas en lumière de tels effets chez *E. angophorae*.

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## Introduction

Environmental factors are potentially of great importance in the evolution and maintenance of social behaviour in the Hymenoptera (Lin and Michener 1972; Evans 1977; Strassmann and Queller 1989; Schwarz et al. 1997; Wcislo 1997). Predation and parasitism pressures, the availability of nesting substrate, and climate can play varying roles in selection for group living and social behaviour, although these factors are often difficult to assess empirically. In univoltine species, removal of climatic constraints on brood development (through climate change or colonisation of new areas) can result in multivoltinism and overlapping generations. This in turn could lower selective thresholds for alloparental care in colonies that have female-biased sex ratios, because of high genetic relatedness between female sibs (Hamilton 1964; Trivers and Hare 1976). Several models have been proposed that may result in female bias in univoltine species independently of opportunities for sib rearing (Hamilton 1967, 1979; Seger 1983; Grafen 1986; Schwarz 1988*a*, 1994) and that could facilitate selection for eusociality in populations where generational overlap coincides with female-biased sex allocation.

Studies of halictine bees have revealed a number of instances in which sociality of conspecific populations fluctuates with changes in local climatic conditions. This variation has often been attributed to broad-scale climatic variation with latitude or altitude, in that longer active seasons in warmer conditions permit the production of multiple broods and create generational overlap. This in turn can result in the expression of different types of social organisation. For example, *Augochlorella striata* is frequently eusocial in temperate areas (Mueller 1996), but shows a predominantly solitary life cycle at the northern limit of its range (Packer 1990). Similarly, populations of *Halictus rubicundus* and *Lasioglossum* (*Evylaeus*) *calceatum* are univoltine and solitary at high altitudes, whereas nearby lowland populations are eusocial (Sakagami and Munakata 1972; Eickwort et al. 1996; see also Hogendoorn and Leys 1997). Variability in some species need not be limited to the effects of latitude and altitude, annual weather variation can also cause fluctuations. Evidence from a single population of *Halictus ligatus* (Richards and Packer 1995) indicates that variation is also possible on a temporal scale, with yearly fluctuations in climatic conditions leading to changes in sociality.

The allodapine bees are a tribe of progressively provisioning stem-nesting bees found in a wide range of habitats in Australia, sub-Saharan Africa, and southern and southeastern Asia. In Australia, species of the genus *Exoneura* are

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**Fig. 1.** Map of eastern Australia showing the distribution of sites: Mooball State Forest Park (28°25′S, 153°35′E), Washpool National Park (29°30′S, 152°20′E), Kioloa State Forest Park (35°30′S, 150°20′E), and Gembrook National Park (37°55′S, 145°40′E). Mean maximum and minimum monthly temperatures (°C) are given for each locality. Weather data are from the Murwillumbah, Mount Pikapene, Bodalla, and Healsville weather stations, respectively.
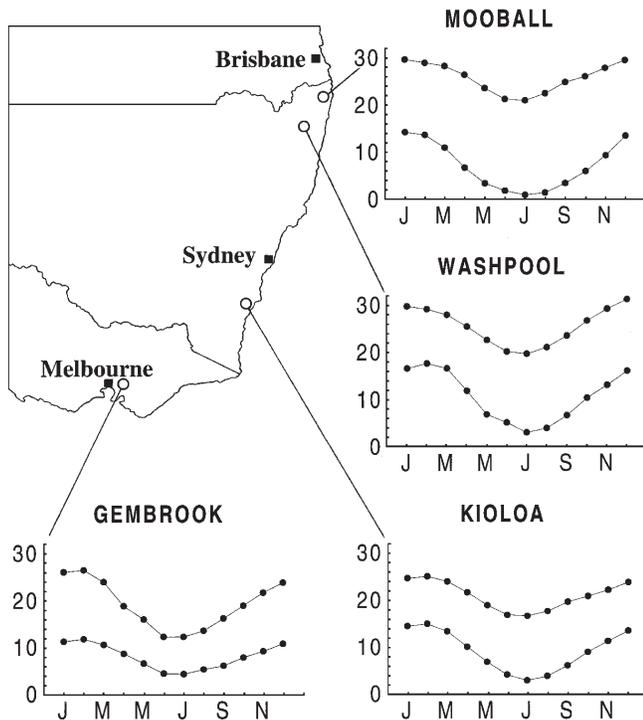


found in a diverse array of habitats from central arid regions to temperate and subtropical coastal, subcoastal, and montane areas. Sociality in studied species varies widely, from eusocial behaviour involving morphologically distinct castes in *Exoneura* (*Exoneurella*) *tridentata* to primitive eusociality in the subgenus *Brevineura* and semi- and quasi-social colonies in *Exoneura* sensu stricto. Species of the latter two subgenera are restricted to the moist temperate areas found along the southern and eastern seaboards and the Great Dividing Range, extending up to the eastern subtropics, and also in southwestern Western Australia. Populations in the southern coastal regions have been the subjects of numerous studies over the last decade (reviews in Schwarz et al. 1997, 1998). These colonies are univoltine and exhibit a subsocial–quasisocial–semisocial polymorphism. Newly emerged adults of *Exoneura robusta* and *Exoneura angophorae* generally overwinter in their natal nest (April–September) and either reuse their natal nest in the following season or disperse in the spring (October–November), usually cofounding nests with close relatives (Schwarz 1988*b*, 1988*c*; Schwarz et al. 1996). However, females often nest with nonrelatives if kin are not available, presumably because of high losses to predation, particularly in small nests (Schwarz and O'Keefe 1991; Bull and Schwarz 1996; Hurst et al. 1997). Egg laying begins in

late winter in reused nests, and larval development may be delayed (up to 6 weeks later in *E. angophorae*; Schwarz et al. 1996). Adult eclosion takes place in mid to late summer. Intracolony relatedness is generally high (newly founded nests: $r \pm SE = 0.597 \pm 0.062$; reused nests: $r \pm SE = 0.485 \pm 0.060$ for *E. robusta*, Schwarz 1987; newly founded nests: $r \pm SE = 0.759 \pm 0.087$; reused nests: $r \pm SE = 0.498 \pm 0.152$ for *E. angophorae*; Schwarz et al. 1996), and sex ratios are female-biased (Schwarz 1988*a*, 1994; Cronin and Schwarz 1997).

Previous studies of *E. angophorae* (formerly referred to as *E. variabilis*; S.G. Reyes, personal communication) indicated that eusociality may be frequent in subtropical Australia (Michener 1965), but these were based on the assumption that nests were founded by single females and that multifemale nests were eusocial. In contrast, southern montane populations of this species (referred to as *E. richardsoni*; S.G. Reyes, personal communication) are predominantly semi-social (Schwarz et al. 1996). Recent studies[2] have shown that small numbers of southern heathland colonies of *E. robusta* produce two broods in a single season, giving rise to opportunities for sib-directed alloparental care. As these species are progressive provisioners, it is possible for a mother to lay a second batch of eggs and die, leaving first-brood females to rear sibs and as a eusocial colony. These data suggest that social behaviour may be labile within these *Exoneura* species, and may be influenced by environmental variables. Although southern populations are constrained to a single brood per season by a short active season, in northern populations, such restrictions are probably relaxed, and the potential exists for multiple broods per season. Newly eclosed females of these species suffer a long latency to reproduction (Schwarz et al. 1998), as adults eclosing in summer do not attain reproductive capability until after a period of overwintering. Hence, there may be selection acting on first-brood females in two-brooded nests to gain assured fitness returns (sensu Gadagkar 1990, 1991) by rearing sibs prior to overwintering in the absence of direct reproductive opportunities. This could lead to eusociality in populations freed of climatic constraints that limit them to a single brood. Our study investigates the life cycles of *E. angophorae* and *E. robusta* over the latitudinal range of their distribution, and has the aim of elucidating the effect of climatic variation with latitude on sociality in these species.

## Methods

### Study sites

Four sympatric populations of *E. robusta* and *E. angophorae* were studied along the eastern coast of Australia, over a range of approximately 10° of latitude, during the period April 1995 to February 1996. Location and climate details for the populations studied are summarised in Fig. 1. Sites were selected with the criteria that (*i*) both species occurred sympatrically, (*ii*) nesting material was consistent between sites (i.e., bees nested in fern fronds), (*iii*) habitats were superficially similar in that they comprised wet montane sclerophyllous forests, and (*iv*) sites were separated from one another latitudinally. Climatic conditions ranged from subtropical in the north to temperate in the south. Sites were dispersed

**Table 1.** Number of foundresses in trap nests at all sites throughout the study for *E. robusta* and *E. angophorae*.

| Location | 1995 | | | | | 1996 | Min./max. no. of foundresses |
|---|---|---|---|---|---|---|---|
| | 9–12 Apr. | 9–12 June | 17–21 Aug. | 22–25 Oct. | 12–19 Dec. | 15–19 Feb. | |
| *E. robusta* | | | | | | | |
| Mooball | 0 | 0 | 2±1.15 (3) | 2.61±0.22 (33) | 3 (1) | 3±1 (2) | 1/6 |
| Washpool | 0 | 0 | 0 | 2.47±0.36 (17) | 1.86±0.34 (7) | 0 | 1/7 |
| Kioloa | 0 | 1 (1) | 0 | 1 (1) | 0 | 0 | 1/8 |
| Gembrook | 0 | 0 | 0 | 0 | 2 (1) | 0 | 2/2 |
| *E. angophorae* | | | | | | | |
| Mooball | 0 | 0 | 0 | 0 | 1 (1) | 0 | 1/1 |
| Washpool | 0 | 0 | 0 | 1.86±0.26 (7) | 1 (1) | 1.67±0.33 (3) | 1/3 |
| Kioloa | 0 | 0 | 0 | 1.25±0.25 (4) | 0 | 1.5±0.29 (4) | 1/2 |
| Gembrook | 0 | 0 | 0 | 1.50±0.22 (10) | 1.75±0.25 (4) | 1 (1) | 1/3 |

**Note:** Values are given as the mean ± SE and values in parentheses are the number of trap nests recovered out of approximately 200 set out per site.

along the eastern seaboard and the Great Dividing Range from northeastern New South Wales to southern Victoria and encompassed the known range of *E. robusta*. *Exoneura angophorae* has been found up to approximately 200 km north of the northernmost locality we used.

Sites were in montane regions where bees nested predominantly in dead fronds of the tree fern *Cyathea australis*. These fronds usually remain suitable for nesting for several years, and form aggregated "skirts" around the base of tree ferns that are added to annually as fronds senesce (Schwarz 1986; A.L. Cronin, personal observation). Habitats were characterised by a tall *Eucalyptus* overstory, with dense understories interspersed with patchily distributed stands of tree ferns. At Mooball (northern New South Wales (N.S.W.)), *Lantana camara* was common along roadsides, and overstories were interfused with palm trees (*Livistona australis*). At Kioloa (southern N.S.W.), tree ferns were more highly aggregated and often formed dense fern gullies. At Mooball, Washpool (mid-northern N.S.W.), and Gembrook (southern Victoria), nesting substrate was almost always used by bees when suitable (not too old or wet) and may have been limiting. At Mooball, *L. camara* provided a secondary nesting material for both species, and blackberry (*Rubus fruticosa*) was a secondary nesting substrate in Gembrook. In Australia, both *L. camara* and *R. fruticosa* are introduced weeds.

### Collections

Nests were collected by gathering occupied fronds up to 50 m from access roads. Samples were collected during 1995 at bimonthly intervals, to investigate the life cycle over a 1-year period. Sampling periods were 9–12 April 1995, 9–12 June 1995, 17–21 August 1995, 22–25 October 1995, 15–19 December 1995, and 15–19 February 1996. Nests were collected at dawn or during inclement weather, when bees were inactive and it could be assumed that all occupants were within the nest.

Intact nests were collected by removing whole fronds and plugging nest entrances with cotton wool. Samples were kept at ~8°C in insulated boxes until nests were opened and contents recorded. Nest occupants were censused, with larvae scored as either small (first or second instar), medium (third to early fourth instar), or large (mid to late fourth instar).

### Trap nests and scoring nest age

Trap nests were used to examine nest founding behaviour. Trap nesting used the methods of Schwarz (1986) and consisted of applying spots of paint to dead fern fronds that did not contain nests and could be collected on subsequent trips when occupied. In this manner, it was certain that nests were newly founded and not reused ones from the previous season. New nests of *E. robusta* and *E. angophorae* are difficult to discern from reused nests on the basis of colony size, as new nests are often cofounded by more than one female, and a new season's females are indistinguishable from a previous season's females soon after the former eclose. Nest age could be determined to some extent by the colouring of the nest lumen: nests from the previous season were stained by food and faeces, but colouration varied with location and season and was not always a reliable guide. It was therefore possible to be sure of nest age only when data were from trap nests. Nests where age could not be determined were termed nests of unknown age, and this group most likely included both newly founded and reused nests.

## Results

### Founding patterns

We examined colony founding patterns to determine if there were any differences in founding behaviour between populations. Nest founding occurred primarily during October in all populations, but there was variation between sites and between species (Table 1).

The earliest recorded newly founded *E. robusta* nest was found at Kioloa in June. New-nest initiation at Mooball may slightly precede that at Washpool, with some new nests being founded in August, but almost all new nests (80%) were recovered in October from both sites. Data from Kioloa and Gembrook are few for *E. robusta* ($n = 2$ and 1 nests, respectively), but previous data for southern montane populations near Gembrook (Schwarz 1986, 1987) are similar to data presented here for Washpool, and indicate that new nests are initiated in spring. There are no data to indicate that dispersal occurred earlier in northern populations, as might be expected if warmer conditions supported earlier activity. Two trap nests recovered from Mooball in February contained late-stage brood (pupae or prepupae), indicating that these nests were established soon after the previous collection (in December) or were not recovered in the previous collection.

The first newly founded nests for *E. angophorae* were recovered in October at all sites except Mooball, where this species was uncommon. Data from the southernmost three sites do not suggest that there is any effect of latitude on the timing of new-nest initiation, and this was similar for all sites. All eight trap nests recovered in February did not con-

**Table 2.** Number of eggs, larvae, pupae, and callow females per nest for all collections and study sites for *E. robusta*.

| Brood stage | Location | 1995 | | | | | 1996 |
| | | 9–12 Apr. | 9–12 June | 17–21 Aug. | 22–25 Oct. | 12–19 Dec. | 15–19 Feb. |
|---|---|---|---|---|---|---|---|
| Egg | Mooball | 0 | 0 | 0 | 2.93±0.73 | 4.80±1.87 | 1.17±0.42 |
| | Washpool | 0 | 0 | 1.85±0.88 | 5.6±1.1 | 3.00±0.70 | 0 |
| | Kioloa | 0 | 1.22±0.91 | 2.75±1.80 | 2.5±1.0 | 1.00±1.00 | 0 |
| | Gembrook | 0 | 0 | 0.13±0.13 | — | 6.25±2.39 | 0 |
| Larva | Mooball | 0 | 0 | 0 | 3.36±0.49 | 2.30±0.94 | 1.44±0.48 |
| | Washpool | 0 | 0 | 0 | 1.28±0.98 | 2.38±0.51 | 0 |
| | Kioloa | 0.14±0.14 | 0.11±0.11 | 0 | 2.73±1.71 | 4.00±1.00 | 0 |
| | Gembrook | 0 | 0 | 0 | — | 0.50±0.50 | 0.07±0.07 |
| Pupa | Mooball | 1.38±0.82 | 0 | 0 | 0.18±0.10 | 0 | 1.44±0.62 |
| | Washpool | 0 | 0 | 0 | 0 | 1.51±0.49 | 0 |
| | Kioloa | 0.29±0.18 | 0 | 0 | 0 | 0 | 0 |
| | Gembrook | 0 | 0 | 0 | — | 0 | 0 |
| Callow female | Mooball | 1.25±0.84 | 0 | 0 | 0.02±0.02 | 0 | 0.44±0.23 |
| | Washpool | 0.36±0.20 | 0 | 0 | 0 | 0.16±0.11 | 0 |
| | Kioloa | 0.86±0.70 | 0 | 0 | 0 | 0 | 0 |
| | Gembrook | 0 | 0 | 0 | — | 0 | 0 |

**Note:** Nests containing parasites (*Inquilina* spp.) are not included. Values are given as the mean ± SE.

tain any brood older than egg stage. These data indicate that there may be a second period of dispersal in *E. angophorae* or that the duration of the dispersal period is longer than that for *E. robusta*.

We tested for differences in cofoundress number between samples and locations using a two-way ANOVA, with the number of cofoundresses as the dependent variable and location and sampling date as factors. ANOVA indicated no significant difference in foundress numbers between sites or samples for either species (*E. robusta*: $F_{[4,61]} = 3.45$, $p = 0.426$ for sample and $F_{[3,61]} = 0.95$, $p = 0.479$ for location; *E. angophorae*: $F_{[2,26]} = 0.23$, $p = 0.808$ for sample and $F_{[3,26]} = 0.17$, $p = 0.913$ for location). We also tested for differences in the proportions of nests founded by single females between sites, as these are the most susceptible to brood failure (Bull and Schwarz 1996). Chi-squared tests revealed no significant effect of sampling date or location on the proportion of singly founded nests for either species (*E. robusta*: $\chi_3^2 = 2.47$, $p = 0.65$ for sample and $\chi_3^2 = 4.66$, $p = 0.20$ for location, $n = 70$; *E. angophorae*: $\chi_3^2 = 0.02$, $p = 0.99$ for sample and $\chi_3^2 = 2.36$, $p = 0.50$ for location, $n = 35$).

**Colony size**

We examined colony size during brood rearing to determine if colony size varied with latitude. Data used for analyses were from samples taken in October and December, after the major period of dispersal and when nests contained females of a single generation and no newly eclosed adults. Trap nests and nests classified as "new" (by colouration of the nest lumen) were excluded from the analyses, although it is likely that some newly founded nests were included in the analyses as nests of unknown age (see Methods). Colony sizes varied from 1 to 15 females for *E. robusta* and from 1 to 11 females for *E. angophorae*. To determine if colony size varied between sites, a two-way ANOVA was performed on colony size of *E. robusta*, with sampling date and site as factors. ANOVA revealed no significant effect of site or sampling date on colony size during brood-rearing season

in *E. robusta* ($F_{[1,63]} = 0.99$, $p = 0.358$ for sample and $F_{[3,63]} = 0.41$, $p = 0.757$ for site). Data for *E. angophorae* could not be transformed to meet the assumptions of ANOVA and, hence, nonparametric analyses were performed separately for each sample date. Unfortunately there were no data from Mooball for December. Kruskal–Wallis nonparametric ANOVAs indicated no effect of location on colony size for either sampling period for *E. angophorae* ($\chi_3^2 = 4.822$, $p = 0.185$ for October, $\chi_2^2 = 2.794$, $p = 0.247$ for December).

**Life cycle and brood rearing**

*Exoneura robusta*

Timing of egg laying and duration of brood development in *E. robusta* varied over the populations studied, but did not appear to conform to expected latitudinal trends. However, as samples were taken at 2-month intervals, timing of egg laying and longevity of brood stages could not be determined exactly. Eggs were first found in the nest in early spring (October) at Mooball, the northernmost locality, but were found in the August sample at Washpool and earlier still at Kioloa, where eggs were found in June (Table 2). No data were available from Gembrook for October, but previous collections from the region near Gembrook (Schwarz 1986) showed that egg laying begins in late August. These data suggest that egg laying did not begin earliest at the northernmost localities. Egg laying in newly founded nests could not have begun begin until October, subsequent to the major period of dispersal and the founding of new nests. However, our data indicate only a single period of egg laying, suggesting that the timing of egg laying in newly founded nests overlaps with that in reused nests.

The onset of larval eclosion was more uniform over the latitudinal range; however, we again rely on other data for Gembrook that suggest that eclosion occurs in October or early November (Schwarz 1986). At all other sites, larvae were present in nests in October. Timing of pupation also differed, with the first pupae being found at Mooball in

**Table 3.** Number of eggs, larvae, pupae, and callow females per nest for all collections and study sites for *E. angophorae*.

| Brood stage | Location | 1995 | | | | | 1996 |
| | | 9–12 Apr. | 9–12 June | 17–21 Aug. | 22–25 Oct. | 12–19 Dec. | 15–19 Feb. |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Egg | Mooball | 0 | 0 | 9.57±4.99 | 0 | 3.00 | 3.33±1.76 |
| | Washpool | 0 | 7.29±1.14 | 10.37±1.15 | 3.30±0.91 | 4.60±1.19 | 0.22±0.22 |
| | Kioloa | 0 | 5.61±1.36 | 5.91±1.67 | 3.67±1.41 | 5.45±1.19 | 0.11±0.11 |
| | Gembrook | 0.22±0.15 | 6.76±1.04 | 6.35±1.41 | 1.70±0.55 | 4.38±0.65 | 0 |
| Larva | Mooball | 2.00±2.00 | 0 | 0.57±0.57 | 0 | 0 | 1.33±0.88 |
| | Washpool | 0 | 0.03±0.03 | 0.81±0.29 | 2.40±0.68 | 5.1±1.82 | 0.22±0.22 |
| | Kioloa | 0.07±0.07 | 0.17±0.09 | 0.91±0.34 | 1.00±0.52 | 0.82±0.46 | 0.21±0.21 |
| | Gembrook | 0 | 0 | 0 | 1.40±0.61 | 4.71±1.05 | 0 |
| Pupa | Mooball | 3.00±3.00 | 0 | 0 | 0 | 0 | 3.00±1.53 |
| | Washpool | 0 | 0 | 0 | 0 | 2.80±1.33 | 0.78±0.78 |
| | Kioloa | 1.14±0.51 | 0 | 0 | 0 | 3.64±1.36 | 0.21±0.21 |
| | Gembrook | 0.33±0.23 | 0 | 0.04±0.04 | 0 | 0.48±0.26 | 1.33±0.55 |
| Callow female | Mooball | 1.00±1.00 | 0 | 0 | 0 | 0 | 0 |
| | Washpool | 1.67±1.67 | 0 | 0 | 0 | 0.20±0.13 | 0 |
| | Kioloa | 0 | 0.11±0.11 | 0 | 0 | 0.09±0.09 | 0 |
| | Gembrook | 0 | 0.04±0.04 | 0.04±0.04 | 0 | 0 | 0.11±0.11 |

**Note:** Nests containing parasites (*Inquilina* spp.) are not included. Values are given as the mean ± SE.

October, followed by Washpool in December, Gembrook in February, and Kioloa in April. However, it is likely that pupation began at Kioloa in February, as pupae are found at the more southerly Gembrook site at this time, and the indication of late pupation at Kioloa may be an artifact of small sample size. Callow females were first found at Mooball in October, at Washpool in December, and at Kioloa in April. No newly eclosed adults were found at Gembrook, but other data indicate that adult eclosion takes place toward the end of February (Schwarz 1986). Our data suggest that brood-development rates varied between sites, as timing of egg laying did not closely predict timing of adult eclosion. Adult eclosion appears to take place earliest at the northern localities, although initiation of egg laying is earliest at Kioloa, indicating that brood-development rates may be higher in northern populations.

*Exoneura angophorae*

This species was uncommon in Mooball and hence sample sizes were extremely small for the most northerly site. Egg production in *E. angophorae* began in winter (Table 3), with eggs found in June at all locations except Mooball (but the large numbers of eggs found at Mooball in August suggest that this may be an artifact of the small sample size in June). In contrast with *E. robusta*, colonies of *E. angophorae* at all sites exhibit bimodal egg production, with a second peak in December, although sample sizes for Mooball are small.

In addition to egg laying, the timing of larval and pupal development in *E. angophorae* is also very similar between sites, with pupae found in December at all sites except Mooball. Adult eclosion (appearance of callow females) occurred in December at Washpool and Kioloa and in February at Gembrook (data for Mooball are limited), suggesting that there may also be a weak effect of latitude on brood-development rates in *E. angophorae*. However, differences in timing of brood development between sites are less pronounced than in *E. robusta*.

**Opportunities for sib rearing**

Opportunities for sib rearing are precluded in southern montane *E. robusta* by lack of generational overlap. However, it has been shown that opportunities for sib rearing arise in a southern Victorian heathland population of this species, where a small proportion of colonies produce a second brood in late summer (see footnote 2). First-brood females eclose into adults at this time, giving rise to opportunities for sib rearing and, potentially, eusocial colonies (sensu Michener 1974). Opportunities for sib rearing are also known to occur in southern montane populations of *E. angophorae* (Schwarz et al. 1996). We examined the possibility that latitude influences opportunities for sib rearing in populations of *E. robusta* and *E. angophorae*. The incidence of nests in which opportunities for sib rearing arose was investigated by examining nest census data for nests containing (*i*) both newly eclosed adults or pupae and early dependent brood (i.e., eggs or small larvae) or (*ii*) callow females and any feeding-stage brood (eggs and (or) larvae). Newly eclosed (callow) females are soon indistinguishable from previous generation females, as the former can gain adult pigmentation within a week of eclosion. Moreover, wing wear is not a reliable indicator of age, as this may vary with the behavioural role of the individual (A.L. Cronin, personal observation). Hence, some nests may have contained newly eclosed females that could not be distinguished from previous generation females. As a result, only those nests containing callow females and female pupae could be used to demonstrate clear cases of opportunities for sib rearing, and estimates of proportions of colonies where opportunities for sib rearing occur are likely to be conservative. Colonies fulfilling the above criteria for sib-rearing opportunities are listed in Table 4.

In *E. robusta*, opportunities for sib rearing arose only at the two northernmost sites, Mooball and Washpool, and may result from more rapid brood development at these localities. Proportions of nests where opportunities for sib rearing arose were small at Mooball (<16%), but constituted up to

**Table 4.** Number of nests for which opportunities for sib rearing arose (in bold face in parentheses) relative to the number of nests collected.

| Species | Location | 1995 | | | | | 1996 |
| | | 9–12 Apr. | 9–12 June | 17–21 Aug. | 22–25 Oct. | 12–19 Dec. | 15–19 Feb. |
|---------|----------|-----------|-----------|------------|------------|------------|------------|
| *E. robusta* | Mooball | 8 | 28 | 26 | 46 (**2**) | 10 | 18 (**3**) |
| | Washpool | 11 | 10 | 13 | 18 | 38 (**12**) | 3 |
| | Kioloa | 7 | 9 | 4 | 11 | 3 | 6 |
| | Gembrook | 4 | 6 | 8 | 0 | 4 | 15 |
| *E. angophorae* | Mooball | 2 (**1**) | 2 | 7 | 1 | 1 | 3 (**2**) |
| | Washpool | 3 | 35 | 29 | 32 | 10 (**5**) | 9 |
| | Kioloa | 14 | 18 (**1**) | 11 | 6 | 11 (**7**) | 19 |
| | Gembrook | 18 | 25 (**1**) | 226 | 26 | 21 (**3**) | 18 |
| Total (n/N)[a] | *E. robusta* | 0/30 | 0/53 | 0/51 | 2/75 | 12/55 | 3/42 |
| | *E. angophorae* | 1/36 | 2/80 | 2/81 | 0/65 | 15/43 | 2/49 |

**Note:** Nests containing parasites (*Inquilina* spp.) are not included.

[a]*N*, the sum of nests collected; *n*, the sum of nests where the opportunity for sib rearing arose.

32% of nests collected at Washpool. In *E. angophorae*, some nests with opportunities for sib rearing were found at all sites, and proportions of these nests were up to 50% of colonies collected. Our sample sizes for *E. angophorae* are small, but data do not suggest any effect of latitude on the frequency of opportunities for sib rearing.

In *E. angophorae*, nests with opportunities for sib rearing were found in April, June, and August, in addition to December and February. As egg laying began in June, pupae and callow females in these nests must have been from the previous season. As most adult eclosion of the first brood occurred in December or February, it is likely that callow females and pupae found in June and August were from the second brood. Hence, in reused nests, the development of the second brood may overlap the production of the first brood in the following season. The single nest collected prior to October from Mooball (in April) contained a small larva, one large larva, and pupae, whereas the four nests collected from other sites at this time (Table 4) contained only pupae or callow females and eggs in addition to adult females. Hence, some of the second brood may overwinter as pupae or callow females.

## Discussion

Our results indicate that a number of life-history traits of both species vary between the populations studied, although variability is generally more pronounced in *E. robusta*. The timing of nest founding varies between sites in *E. robusta* but is similar at all sites for *E. angophorae*. There are, however, no trends to suggest that differences in the timing of dispersal in *E. robusta* are related to climatic variation associated with latitude. Colony size does not differ between latitudinally separated populations for new or reused nests of either species. New nests were cofounded by 1–8 and 1–3 females for *E. robusta* and *E. angophorae*, respectively, numbers similar to those reported in previous studies of southern populations of these species (Schwarz 1986, 1988*b*, 1988*c*; Schwarz et al. 1996).

Egg laying by *E. angophorae* is early relative to *E. robusta*, though the timing of dispersal is similar or later (Table 1). Egg laying in reused and newly founded nests overlaps in *E. robusta*, resulting in unimodal egg production, whereas in *E. angophorae*, egg laying in newly founded nests is temporally distinct from egg laying in reused nests, resulting in bimodal egg production. The onset of egg laying varies with latitude in *E. robusta* but is relatively consistent between sites in *E. angophorae*. However, there are no trends to indicate that variation in the timing of egg laying in *E. robusta* is predicted by latitude. Brood-development rates also vary between populations and do exhibit expected latitudinal trends. In *E. robusta*, brood development is more rapid in northern populations, as evidenced by earlier adult eclosion at northern sites despite a relatively late onset of egg laying. In *E. angophorae*, callow females appear earlier in the two centrally latitudinal populations than in the southernmost population, suggesting that development rates may be relatively fast in more northern populations. However, small sample sizes and lack of data from Mooball for this species provide less persuasive evidence than that available for *E. robusta*.

Increased rates of brood development in northern populations of *E. robusta* presumably arise from higher ambient temperatures in the subtropics. Relatively rapid brood-development rates result in some colonies producing a second brood in mid to late summer. Very few intermediate-stage brood (medium-sized larvae to prepupae) were present in these nests (Table 4), suggesting that a second brood was being produced in summer, when most of the first brood had already reached pupation or eclosed into adults. In *E. angophorae*, opportunities for sib rearing occur in mid to late summer in all populations and do not appear to be climatically mediated, despite evidence of potential climatic effects on brood-development rates in this species. In addition, opportunities for sib rearing in *E. angophorae* appear to arise in autumn and winter (April, June, and August), when eclosion of second-brood females overlaps with egg laying in reused nests. However, these overwintering colonies almost certainly consist entirely of same-generation females (i.e., adults from the first and second broods), as the previous season's reproductive individuals are unlikely to survive for a second season (Schwarz et al. 1996). As a result, there is no overlap of generations at this time, as egg layers and newly eclosing females are of the same generation, and there is no opportunity for second-brood females to rear sibs. Instead, these females have the option of dispersing or remaining to help rear nieces and nephews, similar to opportunities

for first-brood females that have overwintered as adults. These data indicate that opportunities for sib rearing occur only during summer in both species, when first brood adult eclosion overlaps with the production of a second brood.

Variation in opportunities for sib rearing between sites in *E. robusta* suggests that climate may mediate opportunities for sib rearing in this species. Sample sizes for *E. angophorae* were often small, and more extensive collections during spring and summer may reveal differences between populations in the proportion of colonies that exhibit opportunities for sib rearing. Sample sizes from southern localities for *E. robusta* are smaller than those from northern sites, and it is possible that small proportions of two-brood nests exist in the former populations but were not detected. Nevertheless, our data also suggest that brood-development rates in *E. robusta* are climatically mediated, and are important in giving rise to opprtunities for sib rearing. In addition, proportions of doubly brooded nests are high (~39%) in some collections of northern populations of *E. robusta*, whereas they are unrecorded in southern montane populations, despite more than a decade of work (Schwarz 1986, 1994; M.P. Schwarz, unpublished data).

Silberbauer and Schwarz (1995) argue that periods of transient eusociality are likely to occur in heathland populations of *Exoneura nigrescens* (misidentified as *Exoneura bicolor*; Schwarz et al. 1998), where opportunities for sib rearing occur in a small proportion of colonies. Moreover, Bull and Schwarz (1997) demonstrated that sib rearing does occur in experimentally orphaned colonies of this species. Another study (see footnote 2) suggests that sib-rearing behaviour is also likely to occur in a heathland population of *E. robusta* in which a proportion of nests is doubly brooded. In these instances, selection for sib-directed altruism could be facilitated by the potential for gaining assured fitness returns (Gadagkar 1990, 1991). First-brood females are unable to lay eggs until the following season and, thus, have a long latency to reproduction (Schwarz et al. 1998). As a result, there is potential for newly eclosed females to gain indirect benefits by helping to rear sibs at a time when there is no option of becoming reproductive themselves. Our data indicate that opportunities for sib rearing arise in northern populations of *E. robusta* and are found in all populations of *E. angophorae*; it is also likely that sib-directed altruism is found in these populations. However, previous studies of allodapines (Michener 1965) are likely to have overestimated the incidence of eusocial colonies, because multifemale colonies were assumed to comprise mother–daughter associations.

Our results indicate that variation in the timing of dispersal and egg laying is often not consistent with expected latitudinal trends and suggest that other factors may be involved. A recent study (see footnote 2) found that opportunities for sib rearing occurred in a heathland population of *E. robusta*, but were precluded in a montane population at the same latitude, and suggested that habitat effects, such as microclimate variation and floral resources, could potentially influence activity and brood-development rates. Although sites selected here were superficially similar, variation in habitat parameters, such as nesting-substrate distribution and suitability, floral resources, and microclimate, may also influence bee-activity and bee-development rates. Indeed, it

seems likely that sociality is mediated by a mosaic of extrinsic factors, and closer analysis of each habitat is required before the relative effects of these parameters can be assessed.

Our findings show that sociality is highly plastic within some species of *Exoneura* and that it is likely to be under the influence of several extrinsic factors, including broad-scale climate variation and, potentially, more proximate factors pertaining to habitat. This highlights the need for caution when assigning species to behavioural categories, unless sociality in populations over the entire geographic range of the species can be shown to be consistent. Careful analyses of the entire range of social plasticity within a species are clearly required, before comprehensive comparative analyses and examination of evolutionary transitions can be undertaken with confidence.

## Acknowledgements

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