Brood insurance via protogyny: a source of female-biased sex allocation

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Sex allocation patterns and colony productivity are examined in *Exoneura nigrescens*, a social allodapine bee. As for previous studies on Australian allodapine bees, numerical sex ratios were strongly female biased in the smallest broods, but neared equality in larger broods. Local fitness enhancement has been suggested previously to explain female-biased allocation in allodapine bees. Here, we propose an alternative model, the 'insurance model', which predicts protogyny and, as a consequence, female-biased sex allocation in small broods with decreasing bias in larger broods. Because allodapine broods are reared progressively in an open burrow, broods require that adult females be present throughout their development in order to survive to maturity. If mothers invest in daughters (alloparents) first, these daughters can rear younger, dependent brood in cases in which orphaning occurs. If such daughters behave as surrogate mothers, then investment in them by mothers should not be regarded as investment in female sex allocation *per se*, giving rise to apparently female-biased broods. The model predicts a pattern of sex ratios as a function of total brood size that very closely match empirical data from *E. nigrescens*.

Keywords: sex allocation; insurance model; protogyny; allodapine bees

1. INTRODUCTION

Sex allocation has had a key role in evolutionary ecology because it can strongly affect parental fitness. Population sex ratios are usually not expected to deviate from equality (Fisher 1930; Shaw & Mohler 1953), yet some animals show clear sex allocation bias. How can populations deviate from an equal sex ratio when such inequality results in higher fitness returns for the production of the rarer sex than for production of the commoner sex? Several models have been proposed to explain biased sex allocation. The main models to date are: the worker-mediated sex ratio bias model (Trivers & Hare 1976), which was proposed for social haplodiploid species in which conflict over the sex allocation of brood is expected between 'queens' and 'workers', such that worker-like individuals should prefer their mothers to invest in female sibs to whom they are more closely related; the partial bivoltinism model (Werren & Charnov 1978; Seger 1983); the helper repayment model (Gowaty & Lennartz 1985; Emlen *et al.* 1986; Lessels & Avery 1987); and a number of nonlinear fitness return models. Nonlinear fitness returns arise when investment in one sex leads to disproportionately large or small returns per unit of investment, and are usually associated with interactions between close relatives (Hamilton 1967; Werren 1980; Clark 1978; Frank 1987; Schwarz 1988). The main nonlinear fitness return models to date are local mate competition (LMC) (Hamilton 1967; Werren 1980), local resource competition (LRC) (Clark 1978) and local resource (or fitness) enhancement (LRE, LFE) (Frank 1987; Schwarz 1994). In addition, Taylor (1981) presents a more general equation for predicting sex allocation bias that results from differential changes in fitness returns from inter- and intra-sex sibling interactions. His model accounts for both positive and negative fitness interactions between siblings,

and therefore gives some insight into specifically which types of interactions are important under differing conditions.

Here, we present a new model for the evolution of biased sex ratios, the insurance model. This model involves nonlinear fitness returns, but differs from other models in the source of fitness returns and in its predictions about the order in which male and female offspring should be produced. We compare the predictions of this model and other key models with observed sex allocation patterns of an allodapine bee, *Exoneura nigrescens*.

(a) The insurance model

Allodapine bees rear their brood progressively in an unsealed, communal chamber, making brood highly vulnerable to predation and starvation in the event of orphaning (Bull & Schwarz 1996; Schwarz *et al.* 1998). The insurance model hypothesizes that a mother may produce one individual (or more) of the alloparental sex as insurance on the remainder of her brood in the event of her death, followed by a switch to unbiased production of further brood. In species in which females provide alloparental care, insurance via protogyny is expected. When males provide the care, insurance via protandry is expected.

The model assumes, first, that as the number of brood produced by a mother increases, the total amount of foraging effort also increases. Second, it assumes that foraging entails mortality risks, so that the probability of a forager surviving decreases with increased time spent foraging. Third, it is assumed that an immature brood will die if left with no adults to provide food and defence. Fourth, we assume that if a brood is orphaned before all individuals have reached independence, then any older brood that have reached independence will take on alloparental duties and rear or defend remaining immatures. Under these assumptions, if the first member of the brood to reach maturity is of the alloparental sex, then the probability of the remaining immature brood being left

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with no adults to rear and defend them is decreased. Investment in individuals of the alloparental sex followed by random gender allocation might therefore be 'seen' as insurance by mothers on the rest of their brood.

In areas of high predator density or resource constraint in which risks associated with foraging are high, mothers may be selected to produce more than a single 'insurance individual' before going on to produce the remaining, unbiased brood, whereas in areas of relatively low predator pressure and resource constraint, a single 'insurance individual' may be sufficient to ensure that the remaining brood survive to independence. Bull & Schwarz (1997) present evidence that newly eclosed *E. nigrescens* females do rear orphaned siblings in the absence of their mother, and Neville *et al.* (1998) suggest that females from *Exoneurella setosa*, another allodapine bee, may be producing daughters ahead of sons to ensure that an adult female capable of defending the nest is present in case of orphaning. In addition, both Queller's (1989) 'reproductive headstart for workers' hypothesis and Gadagkar's (1990) 'assured fitness returns hypothesis' suggest incentives for early eclosing females to adopt alloparental roles. The assured fitness returns model in particular may provide benefits for alloparental care in bees such as *E. nigrescens*, in which the latency period between a female's adult eclosion and her rearing her own brood to adulthood is likely to range between 10 and 13 months.

Mathematically, if females are the alloparental sex, the expected proportion of males produced (P_m) under the insurance model can simply be derived from the total brood size (B) and the level of insurance expected (i) (in terms of the number of females (or worker sex) the mother produces before she begins producing unbiased offspring). If $B < i$, then P_m always equals zero. If $B \geq i$, then:

$$P_m = 1 - ((B - i/2) + i/B) \quad (1.1)$$

Figure 1 shows the expected sex ratio patterns for 'insurance investments' of one and of two females, respectively, as predicted by the model. Under Taylor's (1981) generic equation, biased investment resulting from insurance via protogyny would be due to positive interactions between daughters, and between daughters and sons, as early investment in daughters may increase survivorship of subsequent daughters and sons, and may also allow mothers to produce more brood than they otherwise would.

2. MATERIAL AND METHODS

(a) *Exoneura nigrescens* life cycle

The allodapine genus *Exoneura* is endemic to Australia. *E. nigrescens* (previously referred to as a heathland population of *Exoneura bicolor*; see Schwarz *et al.* (1998) for a summary of recent nomenclatural changes) commonly nests within the pithy centres of dead flower scapes of the grasstree, *Xanthorrhoea minor*, in southwestern Victoria, Australia. Nests consist of a single, unbranched, undivided and unlined tunnel where brood is laid in a clutch at the base of the nest and progressively provisioned by adult female nestmates, a characteristic trait of the allodapine bees. After brood maturation in summer, newly emerged females either disperse during late summer and early autumn,

Figure 1. Predicted proportion of brood, that are males under the insurance via protogyny model for insurance investments of one and two females.

or delay dispersal until after winter (Silberbauer 1997). However, some females never disperse from their natal nest and remain as colonies of 1–5 females during the brood-rearing period in the following spring and summer. Relatedness within established, or 're-used' colonies is moderately high ($r \approx 0.5$) (Schwarz 1994), and multi-female colonies are common during brood rearing (Schwarz 1994). Although *E. nigrescens* is univoltine, some colonies produce a small second clutch of eggs during midsummer when first clutch females are nearing adult eclosion. Newly emerged females from the first clutch have the opportunity to help rear second clutch individuals, making the colony temporarily eusocial (*sensu* Wilson 1971) (Schwarz 1994). Furthermore, in experimentally orphaned colonies, first clutch females reared second clutch immatures, suggesting that no parental coercion is necessary for such helping behaviour (Bull & Schwarz 1997). Previous data suggest that sex allocation within *E. nigrescens* populations is female biased, and the degree of bias within colonies is inversely proportional to the number of brood (Schwarz 1994). This, combined with the opportunities for sib rearing, makes *E. nigrescens* a particularly interesting model system for sex allocation mediated by social interactions.

(b) Methodology

Intact colonies of *E. nigrescens* nesting in dead flower scapes of *Xanthorrhoea minor* were collected along McRaes Road, in Cobboboonee State Forest, western Victoria on six dates covering the majority of the pupal eclosion period. The collection dates were 28 December 1995 ($n=138$ nests), 9 January 1996 ($n=125$), 18 January 1996 ($n=134$), 30 January 1996 ($n=103$), 8 February 1996 ($n=128$) and 20 February 1996 ($n=120$). All nests were collected during early morning or during inclement weather when all colony members were assumed to be present. Nests were plugged and transported on ice to Flinders University where processing took place.

Processing involved splitting nests longitudinally to remove nest occupants. Nests were categorized as either newly founded (very clean nest walls, clearly newly excavated) or re-used (nest walls dark, stained where previous broods had been reared) and colony composition was recorded, with larvae being categorized as either small (first and second instars), medium (third and early fourth instars) or large (late fourth instar). Prepupae were placed in tissue culture wells and left at room temperature to eclose into pupae. The sex of prepupae that successfully eclosed

was recorded. All pupae present in nests were sexed and had their wet weight recorded. A crude relative age was also recorded for each pupa: completely unpigmented, 0; eyes partially darkened, 1; eyes black but no other pigmentation, 2; thorax partially darkened, 3; thorax black and metasoma beginning to darken, 4; fully pigmented, ready to eclose, 5. Intermediate measures were also recorded. A total of 1419 female and 982 male pupae were scored from the six collections.

3. RESULTS

(a) Colony composition and efficiency

Newly founded nests were only found in the 8 February and 20 February collections and had a mean of 1.19 adult females (maximum 3), and re-used nests from all collections had a mean of 1.92 parental generation females (maximum 7). Colony efficiency was assessed using only re-used nests collected on 28 December 1995, and 9 January, 18 January and 30 January 1996. Colonies collected on 8 February and 20 February were not used as by this time newly emerged females in re-used nests were indistinguishable from previous generation adult females, and new nests present in these collections generally did not contain immature brood (91.4% did not contain brood, $n=93$). *Per capita* brood production (PCBP) was calculated as the total number of brood (eggs, larvae, prepupae, pupae, and callow females) divided by the number of adult females present in the nest, and is shown in figure 2 for colonies of different sizes (colonies with five or more females were pooled). Data were homoscedastic (Levene's test: $F_{4,484}=1.464$, $p=0.212$) and analysis of variance (ANOVA) showed a significant effect of colony size on PCBP ($F_{4,484}=19.045$, $p<0.001$). Scheffe's *post hoc* analysis revealed that mean PCBP in colonies with one female was significantly lower than mean PCBP in colonies with two, three or four females, but was not different from colonies that contained five or more females.

Opportunities for sib rearing (alloparental care) were examined to assess the frequency of colonies that might benefit from 'insurance individuals' in the case of orphaning. Sib-rearing opportunities were assessed for colonies in re-used nests from all collections (new nests generally did not contain immature brood so were not included here). Nests were deemed to enable sib rearing if they contained at least one callow (newly eclosed) female or one female pupa at the same time that they contained at least one larva or egg (i.e. dependent stage immatures). Of the 640 re-used nests collected, 275 (43%) had opportunities for sib rearing on the basis of these criteria. In reality, more nests may have had opportunities for sib rearing, but callow females are only distinguishable from adult females (and thus the parental generation) for a short time before their cuticle becomes fully pigmented. Opportunities for sib rearing generally occurred in colonies with larger broods, as in these cases there was a larger lag time between first-produced and last-produced brood.

Less than 1% of colonies ($n=2$ out of 748 colonies) collected had brood present but no adult females. However, this does not represent the frequency of colonies becoming orphaned, as a large number of excavated tunnels were recovered with no occupants at all. It is expected that an orphaned colony would lose its

Figure 2. *Per capita* brood production ($\pm$ s.e.) as a function of the number of adult females per nest in re-used nests of *Exoneura nigrescens*. For each colony size category, separate points indicate different collection dates (samples were taken on 28 December 1995, 9 January 1996, 18 January 1996 and 30 January 1996).

unguarded brood very quickly to ant predators (Bull & Schwarz 1996).

(b) Sex allocation

The effect of pupal age on wet weight was examined prior to analysis of allocation of resources to each sex. For male pupae, data were homoscedastic (Levene's test: $F_{5,961}=0.85$, $p=0.514$) and a one-way ANOVA revealed a significant effect of pupal age on weight ($F_{5,961}=3.452$, $p=0.004$). A least significant difference *post hoc* analysis revealed that male pupae in age category 5 (fully pigmented, ready to eclose) were significantly lighter than pupae of all other age categories, and that no other age categories differed significantly. This is probably because the late stages of pupal development involve a large amount of metabolic activity. For female pupae, the same analyses were attempted but data were not homoscedastic (Levene's test: $F_{5,1378}=2.607$, $p=0.023$) and could not be made so using transformations. Consequently, female pupal weights from the different age categories were compared using independent sample paired *t*-tests. A total of 21 comparisons were made and α -levels were therefore adjusted using the sequential Bonferroni α -level adjustment (Rice 1989). Of these comparisons, age category 5 was significantly lighter than all other groups, and all other groups did not differ from one another. Consequently, male and female pupae of age category 5 were removed from further analysis, as their weights did not reflect investment in the pupae by adult nestmates in the same way as for pupae of other age categories.

Allocation of resources to each sex was examined by comparing the weights of pupae (age category less than 5) from each sex. Mean male pupal weight (n , s.e.) was 12.103 mg (967, 0.059) and mean female pupal weight

Figure 3. Numerical sex ratios (with 95% confidence intervals) plotted against the total number of pupae per nest (filled circles) and the numerical sex ratio investment predicted by the insurance via protogyny model for a single female insurance (open squares).

(n , s.e.) was 12.608 mg (1384, 0.048). A t -test revealed female pupae to be significantly heavier than male pupae ($t_{2349} = -6.655$, $p < 0.0001$).

Numerical sex ratios were calculated for pupae as the number of male pupae divided by the total number of pupae. Numerical sex ratios (with 95% confidence intervals) are plotted against number of pupae present within a nest in figure 3. This graph also plots the sex ratios predicted for different brood size categories by the insurance via protogyny model for investment into a single 'insurance female'.

(c) *Pupal development order and insurance daughters*

The insurance via protogyny model assumes that parental generation females produce a daughter first (or two or more daughters first if the level of insurance required is higher) followed by unbiased allocation. We investigated the order in which male and female offspring are produced by comparing the stage of pupal development of males and females using their degree of pigmentation as an indicator of relative age. Pupae were ranked for age within each colony according to coloration. If two or more pupae within a colony were tied for rank, they were excluded from further analyses, but if other pupae from the same nest were not tied they were included in analyses. So, for example, if the two oldest pupae in a colony were identically coloured, but the next oldest pupa was different, the sex of the two oldest pupal ranks was undetermined, but the sex of the third oldest pupa was recorded. The sex of the four oldest pupae within each nest was recorded, and any older pupae were pooled into a single category (combining all pupae regardless of tied ranks). The resulting data are summarized in table 1 for the four earliest sample dates. Samples from 8 February and 20 February were not used as here the oldest brood was likely to have eclosed, and either become indistin-

guishable from parental generation adults or have dispersed or died. Sex ratios (proportion of males) of each pupal rank were compared with an unbiased parametric value of 0.5 using binomial tests employing a sequential Bonferroni adjustment (Rice 1989) of α -levels to reduce type I error rates. These data show that nearly all of the oldest brood were female, and that the degree of female bias drops for second oldest pupae and approaches parity thereafter. These results suggest that parental generation females were producing between one and two 'insurance' daughters, followed by unbiased allocation.

4. DISCUSSION

Data presented here show that *E. nigrescens* produces numerically female-biased broods, that the bias decreases as brood sizes increase, and that investment approaches parity in only the largest brood sizes. Male pupae are ca. 96% of the weight of female pupae, suggesting that numerical sex ratios are likely to slightly underestimate the extent of female bias. Data also suggest that the first brood to eclose consists almost always of females, and Bull & Schwarz (1997) show that newly eclosed females will rear their sibs in orphaned colonies. In addition, Bull & Schwarz (1996) demonstrate that females nesting alone often fail to produce any brood at all, and they attribute this to predator pressure at the nest as the solitary female forages. The combination of these results supports the predictions of the insurance model, which suggests that females may produce individuals of the alloparental sex before unbiased production of brood as insurance on their brood in the event of their death. Several other sex-ratio-bias models are now discussed in the light of the results presented here for *E. nigrescens*.

Although worker-mediated sex-ratio bias (Trivers & Hare 1976) was unlikely to be important during the early stages of the evolution of worker-like behaviour (as it requires worker individuals to be present in colonies before the evolution of worker individuals; Crozier 1977), such a factor could influence social behaviour and bias investment towards females once it had already arisen (Nonacs 1986; Mueller 1991; Packer 1994; Sundström 1994). Here, non-reproductive individuals that are present within the nest during the early stages of brood production are from the mother's generation and are therefore likely to be aunts to the mother's brood. Haplodiploid aunts are equally related to their nieces and nephews, and are thus unlikely to bias the brood towards one sex. Therefore, it appears as though worker-mediated sex-ratio bias is unlikely to influence numerical sex ratios in *E. nigrescens*, although investment ratios in later-eclosing brood may be influenced by alloparents.

The partial voltinism model (Werren & Charnov 1978; Seger 1983) suggests that female bias may evolve in situations in which males survive for long enough to mate with females from their own generation as well as the next. This model is not applicable to *E. nigrescens* (or to other *Exoneura* species; Schwarz 1994; Cronin & Schwarz 1997) because males do not survive for long enough to mate with females produced during the following season. Although some colonies of *E. nigrescens* produce a partial second clutch, these eggs are laid by the original parental female(s) and egg production by females produced from

Table 1. Number of females and males, and the sex ratios for the oldest, second oldest and subsequent pupae in nests, for four sample dates.

(Pupae whose developmental rank was tied are excluded from the first four developmental ranks, but all pupae whose rank is fifth or older are pooled into a single category, regardless of the existence of tied ranks. Sex ratios (proportion of males) were compared against $r=0.5$ using binomial tests and sequential Bonferroni adjustment of α -levels. ***signifies $p < 0.001$ and **signifies $p < 0.01$ prior to adjustment. Other values are non-significant).

pupal rank and sex ratio (r)	collection dates							
	28 December		10 January		18 January		30 January	
	f	m	f	m	f	m	f	m
oldest pupae	47	2	34	5	33	10	22	4
sex ratio	0.0408***		0.1282***		0.2326**		0.1538**	
second oldest	30	2	18	3	38	13	24	4
sex ratio	0.0625***		0.1429**		0.2549**		0.1429***	
third oldest	15	9	11	11	25	15	13	10
sex ratio	0.375		0.50		0.375		0.4348	
fourth oldest	2	5	9	8	18	10	11	5
sex ratio	0.7143		0.4706		0.3571		0.3125	
remaining pupae	58	72	64	59	95	111	29	37
sex ratio	0.5538		0.4797		0.5388		0.5606	

either clutch does not commence until the following season.

Nonlinear fitness return models suggest that biased sex ratios can arise when the progeny of one sex interact in ways that alter their mean fitness, thus adjusting the reproductive returns obtained from investment in that sex (Crozier & Pamilo 1996). LMC (Hamilton 1967) proposes that the value of sons can be diminished in situations in which brothers compete for mates, and therefore, that mothers should produce a female-biased brood. This model is not relevant to *E. nigrescens*, because males are not philopatric, mating occurs outside the nest, and a considerable portion of matings occurs after winter (by which time brothers are likely to be spatially separated). There is no evidence of inbreeding in populations of *E. nigrescens* (Schwarz 1994), which would be likely to arise if philopatry were significant. LRC (Clarke 1978; Charnov 1982) suggests that the value of daughters should diminish if the daughters compete with each other for limited resources, and therefore predicts male biases among larger brood categories. The data presented here for *E. nigrescens* suggest that although larger broods become less female biased, they never become male biased, and interactions between daughters appear to lead to positive, not negative, fitness returns, at least in cases in which the number of females nesting together is less than five. LRC therefore appears unlikely to be influencing sex allocation patterns in *E. nigrescens*.

LFE (Schwarz 1994) has been used to explain female-biased allocation patterns for *Exoneura robusta*, *E. nigrescens* (Schwarz 1988, 1994) and *Exoneura angophorae* (Cronin & Schwarz 1997). LFE in allodapine bees was suggested because large benefits accrue during spring and early summer when same-generation females cooperate to rear brood. LFE predicts strong female bias in small broods and less bias in larger broods once an optimal number of cooperating females has been reached. Data presented here support the hypotheses of LFE in that the strongest female biases were observed in the smallest broods and

biases became progressively smaller as brood size increased, and interactions between female nest-mates resulted in increased brood-rearing efficiency in colonies of up to four females. However, although LFE predicts greater levels of female bias in smaller clutch sizes, the mechanisms leading to positive fitness interactions suggested for LFE (Schwarz 1988, 1994) and the order of brood production are different from that suggested by the insurance via protogyny model proposed here. Under Taylor's (1981) generic equation, LFE suggests that positive interactions between daughters can increase mean daughter fitness, whereas the insurance model suggests that early investment into alloparental individuals can minimize direct fitness losses to mothers via positive interactions between daughters, and between daughters and sons. Although LFE and the insurance model predict similar overall investment curves, the insurance model specifically predicts investment in individuals of the alloparental sex before unbiased brood production, whereas LFE is not specific about the order in which each sex is produced.

The helper repayment model (Gowaty & Lennartz 1985; Emlen *et al.* 1986; Lessels & Avery 1987) also predicts a bias towards the 'worker' sex. Under this model, the investment in helpers or worker-like individuals is effectively repaid, so that investment in such individuals is not counted as sexual investment, as it is seen as 'repayment' for the work that these individuals do. Although the helper repayment model predicts biased investment towards the 'worker' sex, the order of investment in each sex is not specified.

In conclusion, results presented here support the notion that insurance against brood loss via early production of females could lead to female-biased allocation ratios. However, two alternative models, LFE and the helper repayment model, may also be important for such biased allocation, and these models may not be mutually exclusive. Here, mothers are clearly producing one or two daughters (alloparents) before the production of unbiased

brood and this may be important in decreasing fitness losses to mothers by insuring against predation in the event of colony orphaning.

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